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Impacts of Natural and Anthropogenic Colonized Habitats on the Range Shifting Mangrove Tree Crab (Aratus Pisonii)

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IMPACTS OF NATURAL AND ANTHROPOGENIC COLONIZED HABITATS ON THE RANGE SHIFTING MANGROVE TREE CRAB (*ARATUS PISONII*)

by

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DEDICATION

This dissertation is dedicated to my parents, Greg and Linda, and my fiancée, Aimee for their unwavering love and support. I could not have done it without you.

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ABSTRACT

Mis-matches in climate-mediated shifting rates cause the ranges of some species to become decoupled from their historic ecosystem, leading to the colonization of ecosystems they have not previously inhabited. When this occurs, the shifting species may experience suboptimal conditions which challenge its ability to persist and expand into the novel ecosystem. However, within the colonized ecosystem, shifting species may encounter artificial habitat analogues: artificial habitats that more closely resemble the species' historic ecosystem than the surrounding habitat and which mitigate some of the negative impacts experienced elsewhere in the novel ecosystem. Despite their importance to the ecology, life history, and continued expansion of range shifting species, habitat effects within novel ecosystems are poorly understood. This dissertation explores habitat effects within the context of the range expansion of the mangrove tree crab *Aratus pisonii*. We show that the artificial structure of boat docks acts as a habitat analogue to the historic mangrove ecosystem of this crab and thus alleviates many negative impacts it experiences in the colonized salt marsh ecosystem. Docks mitigate the alteration of ecologically relevant behaviors and, by providing improved thermal and dietary conditions, negative ecological and life history impacts *A. pisonii* otherwise experiences as it colonizes the salt marsh. Through a mechanistic exploration of reproductive potential and fitness, we also show that while the mangrove provides the best reproductive environment for *A. pisonii,* diet-driven differences in maternal reproductive investment allow the dock habitat to increase reproductive potential and fitness over the

surrounding salt marsh. Further, while they fail to fully grant refuge from hurricane disturbances, docks provide a thermal refuge during winter die-backs allowing *A. pisonii* to expand more quickly and further into the salt marsh than would otherwise be possible. Ultimately, this dissertation emphasizes the impact of habitat effects in altering the ecology, life history, and expansion of range shifting species while highlighting the ability of artificial structures to act as habitat analogues and mitigate negative impacts that may otherwise be encountered in colonized ecosystems.

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GENERAL INTRODUCTION

1.1 Introduction

The shifting of species' geographic ranges is one of the most widespread ecological impacts of global climate change (Walther et al. 2002, Sorte et al. 2010). In recent decades, countless species spanning nearly all taxa have been observed undergoing such range shifts (Walther et al. 2002, Sorte et al. 2010). In some instances, mis-matches in shifting rates cause species to expand at a faster rate than the foundation species of the ecosystem with which they are historically associated (Schweiger et al. 2008). When this occurs, the shifting species will likely colonize an ecosystem to which it is ecologically and evolutionarily naïve and which may differ in structure and resource-availability from the ecosystem to which it is adapted. The colonization of such an ecosystem, which is novel to the expanding species, will necessarily expose the range shifter to novel conditions which could have negative impacts on its ecology, life history, and ability to continue shifting its range.

There is abundant literature exploring the impacts of novel species on the ecosystems they colonize (Mooney & Cleland 2001, Salo et al. 2007, Vilá et al. 2011 and references therein). However, there has been relatively little exploration of the impacts experienced by native range shifters as a result of interactions with colonized novel habitats. Colonizations of novel ecosystems by native species are expected to increase as

climate change progresses (Schweiger et al. 2008, Walther 2010). As some of these species will be economically or socially important, understanding how shifting species are impacted by colonized novel habitats should be a growing concern to managers, policy makers, and the public.

Interactions experienced in a novel ecosystem have the potential to impact numerous aspects of a species' ecology, life history, and behavior which can in turn challenge its continued to survival and expansion. Thus, understanding how habitats within colonized ecosystems differ in their impacts is vital to the accurate prediction, modelling, and management of range shifts. Of particular relevance are artificial habitats. Artificial structures (i.e. buildings, telephone poles, roads, boat docks, etc.) are a nearly ubiquitous feature of the modern landscape. Within natural ecosystems that are novel to a colonizing species, artificial structures may provide conditions that are more similar to that species' historic ecosystem than the surrounding habitat. Such analogous habitats, so named as they are in some way analogous to the historic habitat of a species (Lundholm & Richardson 2010), have the potential to provide improved conditions over those experienced by a shifting species elsewhere in the colonized ecosystem which may allow the population to persist and expand more effectively than would otherwise be possible. However, despite their importance, habitat effects of both artificial natural habitats on range shifting species within colonized ecosystems are poorly understood.

In this dissertation, we seek to close this gap in understanding through an examination of the range expansion of the mangrove tree crab *Aratus pisonii*. The northern range expansion of this neotropical arboreal crab has recently outpaced that of the mangroves with which it is historically associated (Rathbun 1918, Warner 1967,

Riley et al. 2014). This has resulted in *A. pisonii* colonizing salt marshes along the southeast Atlantic coast of the US, an ecosystem it has not previously occupied (Rathbun 1918, Warner 1967, Riley et al. 2014). The salt marsh differs greatly in structure and resource availability from this crab's historic mangrove ecosystem and has previously been shown to negatively impact multiple aspects of its ecology and life history (Riley & Griffen 2017). However, *A. pisonii* are also found on boat docks within the salt marsh. Docks superficially resemble mangroves by providing a sturdy, vertical structure under a covered, canopy-like environment. It is thus possible that docks act as a mangrove analogue within the salt marsh and may therefore mitigate some of the negative impacts *A. pisonii* experiences in this colonized ecosystem.

This dissertation furthers our understanding of habitat effects on the ecology, life history, behavior, and expansion of range expanding species, as well as the role of artificial habitats as habitat analogues. It does so by focusing on the following:

CHAPTER 2 explores the impact of a novel colonized ecosystem on *A. pisonii* behavior. Specifically, this chapter investigates how the site fidelity behavior of *A. pisonii* is altered by the colonized salt marsh ecosystem. Differences in this behavior between the salt marsh and mangrove ecosystems are explored through field observations. Further, a mechanistic understanding of both this behavior and the causes of observed differences between habitats are established.

CHAPTER 3 investigates the potential of docks to act as a mangrove analogue and mitigate negative ecological impacts *A. pisonii* experiences in the surrounding salt marsh. It does so by exploring the impacts of habitat type on multiple aspects of this crab's

ecology including behavior, morphology, and energetics. By comparing these measures between the dock and salt marsh habitats, as well as back to conspecifics from the historic mangrove habitat, this study establishes the relative impacts of these habitats on the ecology of *A. pisonii* while determining the potential of docks to act as a habitat analogue within the salt marsh.

CHAPTER 4 expands on the ecological impacts of habitat type explored in CHAPTER 3 by providing a mechanistic understanding of differences in *A. pisonii* reproductive potential and fitness between habitats. This study establishes the relative impact of habitat type on reproduction by examining the quantity and quality of offspring produced. Additionally, this chapter provides a mechanistic understanding of differences in reproduction between habitats through explorations of the quantity, quality, and chemical identity of the reproductive investment.

CHAPTER 5 explores another aspect in which colonized habitats may alter the ability of a species to persist and expand: by providing refuge from disturbance. Through pre and post-storm surveys, this study explores the habitat specific impacts of a hurricane on populations of *A. pisonii* in its historic and colonized ranges. In particular, it examines whether docks provide superior refuge from storm impacts compared to the surrounding salt marsh and compares the impacts experienced by these populations to those in the mangrove ecosystem.

CHAPTER 6 examines how structural differences between mangrove, salt marsh, and dock habitats alter the socially important behavior of ritualistic aggression. This chapter employs behavioral assays to evaluate mechanistic changes in the behavior itself,

as well as alterations to its potential cost, as a function of the habitat structure on which it is performed. Additionally, this study establishes the importance of claw size to this behavior and examines how claw morphology differs between habitats.

CHAPTER 7 explores the ultimate question of whether docks serve to increase the speed and geographic extent of the *A. pisonii* range expansion. The range-edge distributions of *A. pisonii* on docks and in the salt marsh proper, as well as changes to these distributions, are explored via field surveys spanning two consecutive years. Additionally, a mechanistic understanding of over-winter range setbacks in established through an exploration of *A. pisonii* cold tolerance and an examination of thermal data collected from dock and salt marsh spanning the range-edge.

CHAPTER 8 serves as a general conclusion to the dissertation.

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CHAPTER 2

CHANGES IN SPATIAL BEHAVIOR PATTERS BY MANGROVE TREE CRABS FOLLOWING CLIMATE-INDUCED RANGE SHIFT INTO NOVEL HABITAT[1]

[1] Cannizzo ZJ, & Griffen BD. 2016. Changes in spatial behaviour patterns by mangrove tree crabs following climate-induced range shift into novel habitat. *Animal Behaviour*. 121: 79-86.
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2.1 Abstract

Climate-mediated range shifts into eco-evolutionary novel habitats have the potential to alter the ecology and behavior of range expanding species. Of particular concern are behaviors that have a strong impact on the ecology and life history of expanding species. Behaviors that control the spatial patterns of habitat use may be particularly important. We examined site fidelity and foraging foray behavior of the mangrove tree crab, *Aratus pisonii*, in its historic mangrove habitat and the recently colonized eco-evolutionary novel salt marsh. *Aratus pisonii* showed both strong site fidelity to individual trees and a foraging pattern wherein they made foraging forays that decreased in frequency as their distance from the home tree increased; but they displayed neither behavior in the salt marsh. Chemical cues from feces appear to be the mechanism behind site fidelity in the mangrove and may suggest the mechanism for the loss of this behavior in the salt marsh where substrate is regularly submerged, potentially preventing establishment of such cues. The loss of site fidelity may affect the foraging behavior and predation risk of *A. pisonii* in the salt marsh, leading to a shift in its ecology and bioenergetics. As more species are forced to shift ranges into eco-evolutionary novel habitats, it is important to understand how this shift may affect their life history, behavior and ecology in indirect ways.

2.2 Introduction

As the global climate continues to change, species are expanding or shifting their ranges in response, which is often associated with an accompanying shift in ecosystem foundation species (Walther 2010). However, differences in temporal and spatial

responses to climate change can lead to a species outpacing its foundation species and entering an eco-evolutionary novel ecosystem (Schweiger et al. 2008, Walther, 2010). Eco-evolutionary novel ecosystems often differ greatly in structure and in foundation species from the historic habitat of a range shifting species. This results in the exposure of range shifting species to biological and environmental interactions that differ from their historic ecosystem (i.e. novel interactions). These novel interactions have the potential to alter the ecology of both the shifting species and the ecosystem that it has colonized. Similar alterations of ecology have been demonstrated in biological invasions (Gallardo et al. 2016), which parallel climate-induced range shifts in the production of novel interactions. However, the invasion literature focuses mainly on the effects of the invasion on the ecosystem being invaded. This focus is a result of invading species being seen as unnatural because they are often introduced through human intervention. In contrast, in a climate-induced range shift the colonizing species is entering a novel ecosystem without direct human aid. Unlike in the invasion literature, these species are often native species forced or encouraged to shift ranges due to climate change. Thus, the effects of the move into a novel ecosystem upon the range expanding species itself is of concern. Climate-induced colonization of novel habitats is expected to increase as climate change continues (Lenoir & Svenning 2015) and is likely to alter the ecology of both the shifting species and the colonized ecosystem.

A shift by a species into a novel ecosystem may alter its behavior. Aspects of behavior such as foraging, behavioral syndromes and niche construction can alter both the fitness of a species and the ecosystem that it inhabits (Jones et al. 1994, Naiman 1988, Sih et al. 2012). Behaviors that affect how a species interacts with its environment may

be especially important to range shifting species as they colonize novel ecosystems. There are often several interacting behaviors that determine how species interact spatially with their environment, including site fidelity and exploratory/foraging behavior (Evans & Williams 1991). Thus, it is important to understand how these behaviors change in novel ecosystems. Site fidelity is of particular importance as it may govern how a species interacts spatially with its environment by providing an area where an individual spends a large portion of its time and returns after exploratory/foraging forays.

Site fidelity, or philopatry, is the behavior of staying at or repeatedly returning to the same area. It is seen as fidelity to breeding sites (Bollinger & Gavin 1989; Pomeroy et al. 1994, Refsnider et al. 2009) and natal sites to breed (Berven & Grudzien 1990) and to foraging areas (Cannicci et al. 1996, Driggers et al. 2014) and home areas such as dens (Sebastian et al. 2002, Yoshimura & Yamakawa 1988). In addition, site fidelity influences how an organism interacts with its environment through alterations of other behaviors such as foraging (Evans & Williams 1991). Site fidelity is observed in a wide diversity of animal taxa including insects (Ackerman et al. 1982, Fresneau 1985), mollusks (Sebastian et al. 2002), crustaceans (Cannicci et al. 1996, Stone & O'Clair 2002, Yoshimura & Yamakawa 1988), amphibians (Bell 1977, Berven & Grudzien 1990), reptiles (Refsnider et al. 2009, Refsnider et al. 2012), fishes (Driggers et al. 2014, Marnane 2000), birds (Sedgwick 2004, Warkentin & Hernández 1996) and mammals (Hillen et al. 2009, Lowther et al. 2012). Colonization of a novel habitat has the potential to alter site fidelity. If a species' site fidelity is associated with particular structures, then its site fidelity is especially likely to be affected by colonizing a habitat that differs from its historic habitat in structural make-up and foundation species. Site fidelity is often

associated with important ecological and life history events, such as breeding and foraging (Bollinger & Gavin 1989, Cannicci et al. 1996, Driggers et al. 2014, Pomeroy et al. 1994). Thus, disturbances or changes in site fidelity behavior may have unexpected consequences for a population or species.

Here, we examined site fidelity in the arboreal mangrove tree crab, *Aratus pisonii* (Decapoda: Sesarmidae), following its shift into a novel ecosystem in response to climate change. Historically *A. pisonii* was a Neotropical mangrove-associated species (Beever et al. 1979, Rathbun 1918, Warner 1967). However, the climate-driven northward range expansion of *A. pisonii* has recently outpaced that of its historic foundation species, the red mangrove, *Rhizophora mangle*, resulting in an expansion into the eco-evolutionary novel habitat of the salt marshes of the southern Atlantic coast of the United States (Riley et al. 2014a). *Aratus pisonii* is the dominant herbivore of the red mangrove (Feller & Chamberlain 2007) and its ecology and behavior are closely tied to these trees (Beever et al. 1979, Warner 1967), which are absent in the salt marsh. A sesarmid mangrove crab with a similar ecology to *A. pisonii*, the African mangrove tree crab, *Sesarma lepsozoma*, has been shown to display site fidelity to foraging trees (Cannicci et al. 1996). Given the similarities between these two species, we anticipated that *A. pisonii* would also show site fidelity to individual trees in its historic mangrove habitat. However, as these trees are absent in the salt marsh, we anticipated that any site fidelity shown by *A. pisonii* in the mangrove might break down in the salt marsh.

To fully understand how climate change and range shifts affect site fidelity, it is necessary to examine the mechanisms behind this behavior. The mechanisms behind site fidelity often vary widely among species and include visual (Fresneau1985) and chemical

or olfactory cues (Døving et al. 2006). Chemical cues are often implicated and have been hypothesized to be important in the site fidelity and homing behaviors of many aquatic species including sea turtles (Grassman et al. 1984), reef fishes (Døving et al. 2006) and spiny lobsters (Ratchford & Eggleston 1998). Chemical cues have also been implicated in the communication and site fidelity of many terrestrial arthropod species, most notably ants (Greene et al. 2001). Based on observations that feces are abundant on the branches, trunks and prop roots of mangrove trees in areas where *A. pisonii* is found, it is possible that if *A. pisonii* shows site fidelity, it may use chemical cues from its feces to distinguish one area from another.

Site fidelity often interacts with exploratory/foraging behavior to affect foraging distribution (Evans & Williams 1991). The foraging distribution of an important herbivore such as *A. pisonii* is likely to have implications for the ecosystem that it inhabits. Species that display site fidelity are likely to forage more efficiently within a habitat than are coincident species that do not display philopatry (Benhamou 1989). This may occur if an individual has information about the distribution of food near its home site or in its home range (Benhamou 1989). Individuals can decrease foraging time by showing site fidelity to areas near high-quality foraging sites. Yet, this still may not eliminate the periodic need for long forays to explore for higher-quality foraging areas. Thus, we might expect to see forays from the home site of varying distances, with long forays being less likely than short forays (Adams et al. 2004, Aguilera & Navarrete 2011, Coleman et al. 2005). Such a species would also be expected to return to its place of origin, its home site, after each foray.

Despite the possibility of fidelity to individual mangrove trees in its historic habitat, individual *A. pisonii* in the salt marsh find themselves in a habitat devoid of mangroves. The salt marsh is instead dominated by the grass *Spartina alterniflora,* which differs greatly in structure from the red mangrove. Differences between the habitats also may negate or confuse any chemical cues used to identify "home sites". We therefore anticipated that even if *A. pisonii* shows site fidelity in the mangrove habitat, it might show no site fidelity in the salt marsh habitat (i.e. be incapable of doing so), or it might alter its site fidelity behavior in the salt marsh. A change in site fidelity behavior would necessarily alter how *A. pisonii* interacts with its environment and result in differing ecological patterns and interactions from its historic habitat. Thus, in this study, we sought to explore site fidelity behavior of *A. pisonii*, and its mechanisms, in both the historic mangrove and the novel salt marsh ecosystems. We predicted that *A. pisonii* would show site fidelity to individual mangrove trees in mangrove habitat, use its own feces as a cue to maintain site fidelity and make fewer long-distance foraging trips away from home sites. We further predicted that *A. pisonii* would not show site fidelity in salt marsh habitat.

2.3 Methods

2.3.1 Ethical Note

This research met all animal care guidelines of the supporting institutions and conformed to the legal requirements of the United States of America and the state of Florida. Permits and licenses for this study were granted by the Florida Department of

Environmental Protection, the Florida Fish and Wildlife Conservation Commission and the Guana Tolomato Matanzas National Estuarine Research Reserve (GTM).

2.3.2 Site Description

Aratus pisonii were observed at five mangrove forest sites in and around Fort Pierce, Florida, and two salt marsh sites in and around St Augustine, Florida, between May and August of 2015 (Table 2.1). The mangrove sites represent habitat within the historic range of *A. pisonii* while the salt marsh sites represent recently colonized novel habitats (Riley et al. 2014a).

2.3.3 Collection

At each mangrove site, we haphazardly captured five *A. pisonii* by hand and marked the tree from which they were captured with flagging tape. We measured (to the nearest 0.1 mm) and determined sex of all individuals and painted the dorsal carapace of each crab with one of five colors of nail polish to aid in identification. Following a short period of observation to ensure normal behavior, we released all five crabs onto one tree within 10 m of all collection trees but different from any of the trees on which they had been captured. We did this to avoid biasing the interpretation of an individual's site fidelity as it was impossible to know whether an individual was captured on the tree to which it showed fidelity or while on a foraging foray. We collected 35 individual *A. pisonii* from the mangrove and observed their behavior over seven observational periods (Table 2.1).

We used the same methodology for capture of crabs in the salt marsh with some slight modifications due to the difference in habitat. We collected five individual *A.*

pisonii and marked the *S. alterniflora* stalk nearest to the collection site with flagging tape. We recorded the sex and size of each crab and painted the dorsal carapace of each crab with one of five colors of nail polish. After a short observational period, we released the crabs onto separate *S. alterniflora* stalks within 10 m of the collection area. This was done during a rising tide, so that crabs had no access to the sediment, and thus, could not immediately retreat into holes. Due to differences in the behavior of crabs in the salt marsh as compared to the mangrove, this collection and release was repeated each day with different crabs in order to increase observation sample size. During one observational day at Anastasia State Park, nine crabs were captured because of the rapid loss of many of the original five. Additionally, on one of the days at GTM, only three crabs were captured because of the difficulty in locating individuals before the tide rose. Due to these anomalous days, we collected a total of 67 individual *A. pisonii* from the salt marsh (Table 2.1).

2.3.4 Site Fidelity

Each site was observed for a minimum of 3 days (Table 2.1). Each day, crabs were observed from the time they no longer had access to the sediment until the receding tide once again allowed access to the sediment (~6 h depending on site and day). The timing of this observation assured that crabs were not simply hiding in holes or burrows in the sediment as *A. pisonii* climbs out of the water onto nearby structures to avoid aquatic predators. We recorded the location of each crab each day. A crab that was seen to spend the majority of its time on a given tree or area of salt marsh over two or more consecutive days was considered to display fidelity to that tree or area. These were referred to as the “home tree” and “home area” of the crab, respectively. In the salt

marsh, the home area was a 1 m radius area around the *S. alterniflora* stalk where the individual was observed to spend the majority of its time. This represents an area roughly equal to the basal prop root area of a red mangrove. We also recorded the number of consecutive days an individual was observed to spend the majority of its time on its home tree/area. No crab was seen to display fidelity to more than one tree or area over the duration of the study.

Most sites were visited numerous times with intervening periods of no observation. When an individual continued to show fidelity to its previously established home tree/area after such an intervening period, that crab was considered to have displayed fidelity to that tree/area during the intervening time. This period of time was recorded as the number of days a crab used a home tree/area as opposed to the number of days observed. These distinctions were treated as separate variables in analysis. The number of days that each crab was seen on its home tree/area (response variable) was compared to the number of days each crab was sought (time spent at the site of that crab, predictor variable) using a generalized linear model with a negative binomial error distribution. Separate models were run for each habitat. The use of a negative binomial error distribution corrected for over dispersion. While there was still slight over dispersion in the mangrove model (residual deviation = 44.2, $df = 33$), this error distribution minimized over dispersion. In this analysis, we explored whether any difference in site fidelity between habitats or sites was a statistical artefact resulting from differential effort (days sought).

We explored site fidelity of *A. pisonii* in each habitat type by constructing Kaplan–Meyer survivorship curves using days on the home tree/area instead of survival.

The measure of site fidelity is analogous to survival as crabs lose fidelity to their home tree/area at different times over the course of the study much like individuals in a sample population die at different times throughout a survivorship study. Crabs that had not ceased fidelity by the end of the observational period were right-censored in the analysis (Harrington 2005; Klein & Moeschberger 2005). This corrected for the fact that crabs may have continued to show fidelity after the observational period ended. Owing to the use of right censoring, we compared site fidelity from the mangrove and salt marsh habitats using a log-rank test (Mantel 1966) (often referred to as a Mantel–Cox or Mantel–Haenszel test) (Harrington 2005).

2.3.5 Exploration of the Site Fidelity Mechanism

To test the ability of *A. pisonii* to detect its own feces as a mechanism facilitating site fidelity, we collected 10 individual *A. pisonii* from the representative mangrove site Round Island (Table 2.1). These individuals were kept for 1 week in individual plastic aquaria (22.8 × 15.2 × 16.5 cm, l × w × h) containing a finger bowl of unfiltered sea water. During this time, crabs were given fresh *R. mangle* leaves and had their water changed every other day. At the end of the week, we collected the feces from each crab.

On the seventh day of the experiment, we collected terminal mangrove branches (~50 cm long, ~1 cm in diameter), with little or no *A. pisonii* feces, from a representative mangrove site (Pepper Park, Table 2.1) that differed from site where the crabs were collected, thus ensuring that none of the experimental crabs had prior association with the branches used for experimentation. The branches were always cut below the first leaf, then cleaned of all feces with salt water and allowed to dry.

We then placed each crab in a 5-gallon (18.9-litre) bucket with two mangrove branches of similar length and diameter. One branch was kept clean and the bottom 10 cm of the other was covered in the feces of that crab. To avoid contamination, we always handled feces with entomological forceps and cleaned the forceps after each use with 95% ethyl alcohol. The two branches were placed crossing and leaning on the inside of the bucket (Fig. 2.1). The crab was then placed in the bottom of the bucket between the two branches. We recorded which branch each crab chose to climb and then returned the crab to its aquarium. If the crab had not chosen a branch after 15 min, we added a small amount of unfiltered salt water to the bucket to encourage the crab to choose. We then haphazardly changed the position of the branches in the bucket to control for biases in crab choice due to external factors, and we repeated the experiment with the same crab. We performed three trials on each of the 10 crabs in this way. In all but one trial the crab quickly chose a branch when water was added. The trial in which the crab did not choose either branch was dropped from the analysis. In between each crab, we rinsed and dried the bucket to avoid cross-contamination.

To examine the effect of the feces of another *A. pisonii* on the site fidelity mechanism of individuals, we again collected 10 additional *A. pisonii* from Round Island. We used the same methodology as above except that instead of a clean branch, the crab had the choice between a branch with the feces of another individual or their own feces. As before, three trials were run for each individual. Two individuals did not choose a branch during one of their trials and these trials were dropped from the analysis.

We used a generalized linear random effects model with a binomial error distribution to test whether the crabs' choice of branch (with own feces versus clean, and

with own feces versus other crab's feces) differed significantly from random (Agresti 2002). We ran separate models for each experiment. For both experiments, the model was run with choice as the response variable and individual crab as the random effect to account for repeated measures. We then used a linear probability model to determine the likelihood of an individual choosing the branch with feces as opposed to a clean branch. We did this by applying an antilogit function ($\frac{1}{1+e^{-\text{intercept}}}$) to the intercept of the model, which acts to back transform the intercept and gives the probability of one outcome occurring instead of the other (Agresti 2002). Thus, this methodology allows for the determination of the likelihood that a crab will choose one branch over the other. We also ran this linear probability model for the second experiment to determine the likelihood of an individual choosing the branch with its own feces as opposed to a branch with feces of another individual.

2.3.6 Foraging Forays

If an individual from the site fidelity study described above displayed site fidelity, we noted forays away from the home tree or area. We recorded the regularity of forays and measured the distance from the home tree or area. The distance of a foray was determined with a measuring tape in a direct line from the trunk of the home tree to the end location of the foray. While crabs must travel along roots and branches and thus do not travel in a straight line, this was done to normalize methodology as the exact path of crabs that travelled through the canopy was either not known or unreachable. This methodology results in the measured distance being shorter than the distance a crab actually travelled. Therefore, the foray distances presented reflect conservative estimates. The proportion of days that an individual was observed to undertake a foray was then

compared to the distance of that foray. Visual observation of the data suggested that the number of forays decreased exponentially with distance from the home site. Thus, we fitted the relationship to an exponential decay using a nonlinear least squares regression.

2.4 Results

2.4.1 Site Fidelity

Aratus pisonii displayed greater site fidelity in the historic mangrove habitat (77.14% of individuals) than in the novel salt marsh habitat (8.95% of individuals) (log-rank test: $\chi^2_1 = 20.8$, $P < 0.001$; Fig. 2.2). This low fidelity in the salt marsh led to the necessity of collecting five new crabs each day of observation, as outlined in the Methods. In addition, many individuals in the mangrove showed fidelity throughout the observational period, with one crab displaying fidelity on at least 88 days. In contrast, most individuals in the salt marsh were unlikely to be seen again, either in the designated area where the crab was released, or in the surrounding marsh more broadly. Those individuals that showed fidelity throughout the observational period were right-censored in the analysis (Fig. 2.2b, d).

The longer a crab was sought in the mangrove, the longer it was likely to be seen on its home tree (GLM: $z_{33} = 0.03743$, $P < 0.001$; Fig. 2.2b). In the salt marsh, individuals were unlikely to be seen again regardless of search effort (GLM: $z_{65} = 0.837$, $P = 0.427$; Fig. 2.2d). This suggests that the difference in site fidelity behavior between the mangrove and salt marsh was not simply a statistical artefact due to differences in the observational periods and sample sizes of the two habitats. In fact, the sample size in the salt marsh was almost twice that in the mangrove and the 1 m radius of the home area of

the salt marsh was larger than the basal area of many mangroves chosen as home trees; both of these factors would make it more likely to find site fidelity in the salt marsh.

2.4.2 Site Fidelity Mechanism

When given the choice between a clean branch and a branch with their own feces, individual *A. pisonii* showed an 88.96% likelihood of choosing the branch with their own feces (GLMM: $z_{28} = 2.202$, $P = 0.0277$). Comparatively, when given the choice between a branch with their own feces and one with feces from another individual, individual *A. pisonii* showed an 80.53% likelihood of choosing the branch with their own feces (GLMM: $z_{26} = 1.901$, $P = 0.0573$).

2.4.3 Foraging Forays

Given the overall lack of site fidelity behavior in the salt marsh, we only explored foraging forays in the mangrove. Two of the 28 individuals that were observed to show site fidelity behavior were dropped from the foraging foray analysis because of uncertainty in the distance travelled during forays, leaving 26 individuals with known foray distance. Despite spending the majority of their time on their home tree, 80.7% of individuals went on forays at some point during the observational period and 73.1% went on forays daily (Fig. 2.3a).

The regularity of a foray (proportion of days undertaken) was related to foray distance via the exponential decay equation

$$\text{Proportion} = C\text{e}^{-k \times \text{distance}}$$

where $C = 1.020 \pm 0.051$ (nonlinear least squares regression: $t_{27} = 19.864$, $P < 0.001$) and $k = 0.053 \pm 0.188$ (nonlinear least squares regression: $t_{27} = 2.833$, $P < 0.01$) (Fig. 2.3a). In addition, as foray distance increased, the number of crabs observed taking such forays decreased (Fig. 2.3b). Note, our measure of foray distance does not reflect the total distance travelled by each crab (because we measured straight-line distances as opposed to actual paths taken by the crabs; see Methods). In addition, crabs are more likely to travel nonlinearly as foray distance increases. Therefore, the distance measured, using our methodology, was biased towards being progressively shorter than the actual distance travelled as foray distance increased. The removal of this bias would progressively increase the distance of the longest forays (longer distances become even longer), making the reported results a conservative estimate. Together, these results support the conclusion that individual *A. pisonii* usually make short-distance foraging forays and seldom make long-distance foraging forays away from their home trees within mangrove habitat.

2.5 Discussion

We have shown that in its native mangrove habitat, *A. pisonii* displays both site fidelity to a home tree and a foraging pattern that may be expected from a philopatric species. However, site fidelity behavior of *A. pisonii* does not appear to be retained in the novel salt marsh habitat. As site fidelity is often associated with important ecological and life history events such as breeding (Bollinger & Gavin 1989, Pomeroy et al. 1994) and foraging (Cannicci et al. 1996, Driggers et al. 2014), the loss of this behavior represents a potential shift in the ecology of *A. pisonii*.

Cues from feces appear to play some role in the site fidelity behavior of *A. pisonii* in the mangrove. This result may also suggest the mechanism behind the loss of this behavior in the salt marsh. Despite the large amount of time *A. pisonii* spent on marsh grasses, little feces were observed on marsh grass stalks. This could be due to submergence of grass stalks at each high tide. Submergence likely cleans any feces from the grasses, preventing cues used by *A. pisonii* from developing. In contrast, in the mangrove, many trees are connected by prop roots and branches, parts of which always remain out of the water, and could thus maintain a cue or cue trail throughout the tidal cycle. As the observation period took place during inundation, the observed foraging pathways were maintained on areas of branches and prop roots that remained unsubmerged. Such out-of-water connectivity is drastically reduced in the salt marsh. Individual *A. pisonii* often entered the water to travel between grass stalks. This lack of connectivity during inundation likely prevents the development of any cue trails in the salt marsh. Thus, it is possible that the loss of site fidelity in the salt marsh is a result of an inability for individuals to establish the cues that aid in this behavior.

The same chemical cues that facilitate site fidelity may also lead to the observed fidelity in daily foraging paths. Chemical cues would allow the establishment of trails to known high-quality food sources as seen in a number of ant species (Aaron et al. 1993, Greene & Gordon 2007) and may suggest route-based navigation, where information on location is generated while in route (Etienne 1987). The potential display of route-based navigation is additionally supported by the result that 18 of the 19 individuals that went on daily forays were observed to always travel to the same place and almost always followed the same path. The 19th individual also travelled to the same area daily but, in

addition to its normal foray, it undertook the longest foray recorded (23 m) on one of the days it was observed. This suggests that individual *A. pisonii* show fidelity to foraging areas and to the paths they take to these foraging areas.

The observed forays also showed a distinct decline in frequency as distance from the home tree increased (i.e. crabs made short forays more often than long forays; Fig. 2.3). Fidelity to a particular tree with nearby high-quality resources would be beneficial and likely result in such a foraging pattern. This conclusion is further supported by the observation that some individuals that made forays fed at the end of the foray. One individual in particular took the same path daily to visit a wooden board trapped in the roots of a mangrove neighboring its home tree. The board was submerged during high tide, but as the tide receded, this individual would leave its home tree and travel to the board where, along with a number of other *A. pisonii*, it would feed. As evidenced by the common use of fouling plates to study mangrove epibenthic communities (Bingham 1992, Bingham & Young 1995, Sutherland, 1980), organisms grow on any hard substrate in the mangrove habitat. These substrates support a diverse fouling community of flora and fauna, including sponges, bivalves, bryozoans, ascidians and arthropods (Bingham 1992, Bingham & Young 1995, Kathiresan & Bingham 2001). *Aratus pisonii* is known to feed on such fouling organisms (Díaz & Conde 1988), and the wooden board to which one of our marked *A. pisonii* travelled daily had a number of these organisms upon it. Additionally, animal protein is an important dietary supplement for *A. pisonii* (Riley et al. 2014b) and, when given a choice, *A. pisonii* preferentially feeds on animal material (Erickson et al. 2008). Thus, the wooden board likely provided easy access to a high-quality food source. Maintaining fidelity to a tree near such a high-quality foraging area

would be energetically beneficial, allowing the individual to spend less time and energy finding food (i.e. reducing the need to explore for potentially more favorable foraging areas via long forays).

While crabs in mangrove habitat clearly made few long-distance foraging forays away from their home tree, this pattern of foraging could reflect a number of exploratory patterns. A decrease in the regularity of steps as distance increases is a characteristic of many random walk models including biased random walks, correlated random walks, Brownian random walks and Lévy walks, among others (Benhamou 2005). In addition, our results suggest that *A. pisonii* foraging movements are driven by fecal cues, which may result in a foraging pattern resembling scent-marking orientation shown to explain mammal movements (Benhamou 1989). However, the purpose of our study was not to identify the precise mathematical form of the foraging patterns displayed by *A. pisonii* but simply to show that they display a foraging pattern that is likely to be closely tied to and affected by site fidelity behavior.

Regardless of the cause, the loss of site fidelity in the salt marsh could have important implications for the ecology and life history of *A. pisonii* in this novel ecosystem. If *A. pisonii* employs site fidelity to maintain favorable foraging sites like other ecologically similar species (Cannicci et al. 1996) and as suggested by the observed foray behavior, loss of this behavior in the salt marsh could lead to loss of favorable foraging sites and increased search time during foraging. Increased search time is energetically detrimental as individuals spend energy attempting to find food as opposed to eating. Additionally, increases in searching and exploration may lead to increased predation risk. While it is unknown whether *A. pisonii* shows site fidelity to predation

refuges, many species do (Branch 1978, Sebastian et al. 2002, Shields 1984). If the loss of site fidelity leads to a loss of fidelity to predation refuges, this would further increase predation risk. It is therefore possible that the loss of site fidelity in the salt marsh could represent a significant alteration to both the behavior and ecology of *A. pisonii*.

It is also possible that the loss of site fidelity behavior represents an adaptation to the novel salt marsh ecosystem rather than a consequence of the inability to establish cues in the marsh. Previous work has found that *A. pisonii* displays smaller size at maturity, lower larval quality and lower fecundity in the salt marsh (Riley & Griffen 2017). This would suggest that the salt marsh is a suboptimal habitat for *A. pisonii*. Thus, it is possible that the loss of site fidelity is an adaptation in response to these negative impacts. Yet, it is difficult to see how abandoning site fidelity would improve these life history characteristics. Addressing these shifts in life history would probably require *A. pisonii* to improve its bioenergetics. However, as argued above, site fidelity is likely to facilitate access to bioenergetically favorable habitat and thus a loss of site fidelity would be more likely to contribute to the observed life history shifts than to counteract them. It is more probable that the loss of site fidelity is a result of novel conditions interfering with this behavior (such as elimination of odor cues). Thus, the loss of site fidelity is more likely to be a mechanism contributing to the suboptimal nature of the salt marsh than an adaptation of *A. pisonii* to counteract negative novel conditions.

As more species are forced to shift ranges into eco-evolutionary novel habitats, it is important to understand how these shifts may affect their life history, behavior and ecology in indirect ways. The change in site fidelity behavior that we have shown in *A. pisonii* demonstrates that the successful response of species to climate change depends on

more than just their ability to shift their ranges fast enough to keep up with rapidly changing environmental conditions. Rather, this work suggests that successful responses to climate change also hinge on the ability of behaviors and other adaptations that have evolved in historic conditions to provide suitable strategies under the novel conditions that arise following range shifts into eco-evolutionary novel habitats. Thus, as climate-mediated range shifts become more common, it will be important to explore changes in the ecology and behavior of the species involved to determine whether behaviors that facilitate success in historical habitats are still viable under the novel conditions that these species now face.

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2.7 Tables

Table 2.1: Observation sites, days observed and total number of *A. pisonii* observed at each site

Site	Habitat	Lat-Long	Observational Periods	Total Days Observed	Crabs Observed
Round Island Park	Mangrove	27°33'33"N 80°19'53"W	5-19, May; 4 Aug	11	5
Pepper Park	Mangrove	27°29'42'N 80°18'12"W	25 May-4 Jun 13-16 Jul	10	10
Oslo Park	Mangrove	27°35'14"N 80°21'55"W	28-30 Jul	3	5
North Causeway Park	Mangrove	27°28'28"N 80°19'12"W	23-30 Jun; 5-7, 10 Aug	9	10
Bear Point	Mangrove	27°25'48"N 80°17'10"W	1-3, 12 Jul	4	5
GTM NERR	Saltmarsh	30°0'49"N 81°20'42"W	20-22 May; 16-21 Jun; 7-9 Jul	12	48
Anastasia State Park	Saltmarsh	29°52'40"N 81°16'32"W	21-23 Jul	3	19

2.8 Figures

Figure 2.1. Set-up of two-choice experiments examining faeces as a mechanism of site fidelity in *A. pisonii*. Two mangrove branches were placed in crosswise fashion in a bucket and an individual *A. pisonii* was placed between them. In one experiment, one branch was treated with the crab's own faeces and the other branch was left untreated (clean). In a second experiment, one branch was treated with the crab's own faeces and the other branch was treated with another crab's faeces. The branch onto which the crab climbed was recorded as its choice.

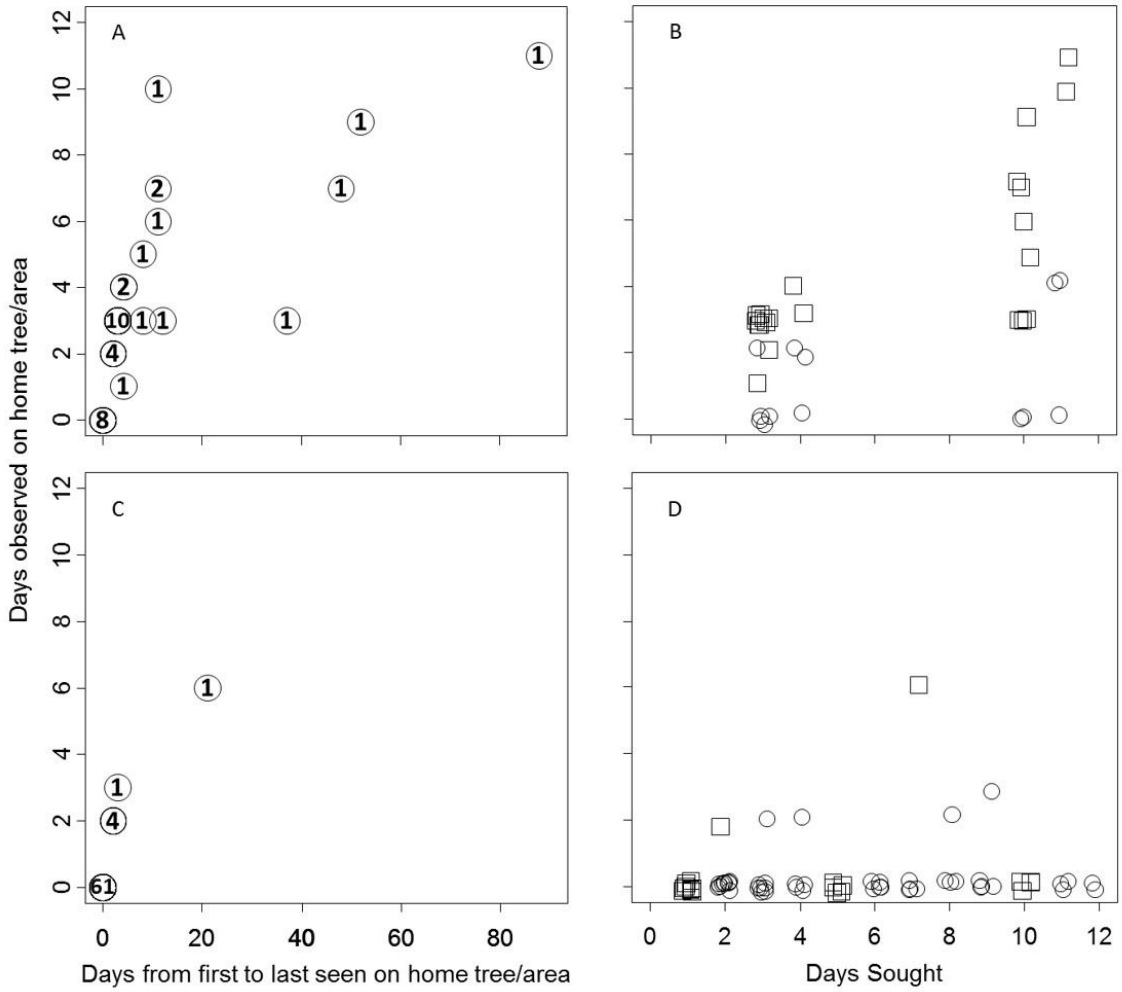

Figure 2.2. Site fidelity in *A. pisonii*. Days observed on home tree/area versus days from first to last seen on home tree/area in the (a) mangrove and (c) salt marsh habitats; numbers within each circle represent the number of data points at that location. The number of days individual crabs were sought and observed in the (b) mangrove and (d) salt marsh are also represented; crabs that were right-censored are represented as squares, with data points jittered to facilitate observation of density.

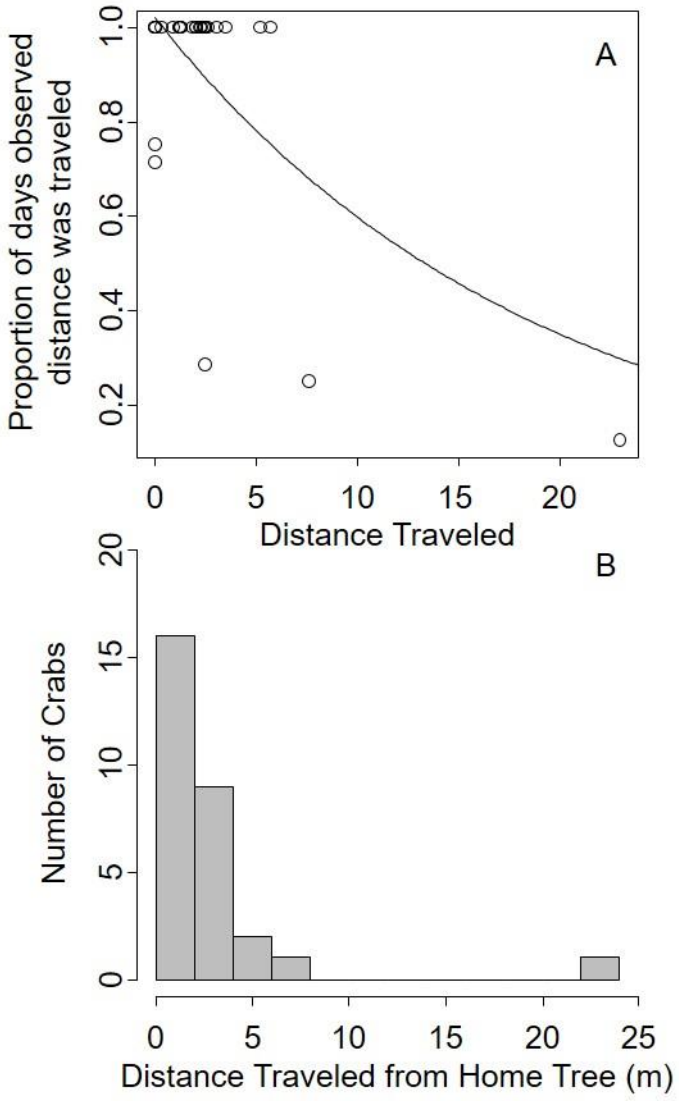

Figure 2.3. Foraging foray behaviour of crabs from the mangrove habitat. (a) Proportion of days that the observed crab travelled a certain distance. The solid line shows the exponential decay from the equation given in the main text (see Results, Foraging Forays). (b) Number of crabs that made forays of particular distances.

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CHAPTER 3

AN ANTHROPOGENIC HABITAT WITHIN A SUBOPTIMAL COLONIZED ECOSYSTEM PROVIDES IMPROVED CONDITIONS FOR A RANGE-SHIFTING SPECIES[1]

[1] Cannizzo ZJ, Dixon SR, & Griffen BD. 2018. An anthropogenic habitat within a suboptimal colonized ecosystem provides improved conditions for a range-shifting species. *Ecology and Evolution*. 8: 1524-1533.
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3.1 Abstract

Many species are shifting their ranges in response to the changing climate. In cases where such shifts lead to the colonization of a new ecosystem, it is critical to establish how the shifting species itself is impacted by novel environmental and biological interactions. Anthropogenic habitats that are analogous to the historic habitat of a shifting species may play a crucial role in the ability of that species to expand or persist in suboptimal colonized ecosystems. We tested if the anthropogenic habitat of docks, a likely mangrove analogue, provides improved conditions for the range shifting mangrove tree crab *Aratus pisonii* within the colonized suboptimal salt marsh ecosystem. To test if docks provided an improved habitat, we compared the impact of the salt marsh and dock habitats on ecological and life history traits that influence the ability of this species to persist and expand into the salt marsh and compared these back to baselines in the historic mangrove ecosystem. Specifically, we examined behavior, physiology, foraging, and the thermal conditions of *A. pisonii* in each habitat. We found that docks provide a more favorable thermal and foraging habitat than the surrounding salt marsh while their ability to provide conditions which improved behavior and physiology was mixed. Our study shows that anthropogenic habitats can act as analogues to historic ecosystems and enhance the habitat quality for range shifting species in colonized suboptimal ecosystems. If the patterns that we document are general across systems, then anthropogenic habitats may play an important facilitative role in the range shifts of species with continued climate change.

3.2 Introduction

Climate change is forcing or encouraging many species to shift their geographic ranges (Walther et al. 2002, Sorte et al. 2010, Canning-Clode et al. 2011). These shifts are often associated with the simultaneous shifts of ecosystem foundation species (Walther 2010). However, differential shifting rates between the ecosystem foundation species and other species in the community can occur and may have cascading effects on community structure and ecosystem function. When such a mismatch in shifting rates occurs, it can result in a species colonizing a new ecosystem which it has never previously inhabited (Schweiger et al. 2008). Colonization of new ecosystems as a result of different shifting rates is expected to increase as climate change continues (Schweiger et al. 2008, Walther 2010).

While there has been abundant discussion on the importance of corridors in aiding range shifting species through increasing habitat connectivity (Hannah 2001, Williams et al. 2008, Heller & Zavaleta 2009, Krosby et al. 2010), little work has been done to determine how these shifts impact the species themselves. This is particularly true of range shifts which result in the colonization of new ecosystems. A range shift into an ecosystem that a species has not previously inhabited exposes the colonizing species to novel biological and environmental interactions. Due to the complexity of these interactions, predicting how they will impact both the colonized ecosystem and the colonizing species can be difficult. The invasion literature contains abundant research on the impact of novel species on colonized ecosystems (Mooney & Cleland 2001, Salo et al. 2007, Vilá et al. 2011 and references therein). Yet, the impact of novel habitats on colonizing species is relatively understudied (but see Phillips et al. 2010), likely because

most studies of novel species-ecosystem interactions are found in the invasion literature where the invader is viewed as unnatural and therefore undesirable.

Among other factors, a colonizing species may find itself in an ecosystem that differs greatly from its historic ecosystem in foundation species, structure, food sources, and environmental stressors. Barring preadaptation (Hamilton et al. 2015), these differences are likely to result in suboptimal conditions for the colonizing species (Holt et al. 2005, Keller & Taylor 2008). In fact, novel biotic and abiotic interactions result in the failure of the majority of introduced species to establish populations (Williamson 1996, Zenni & Nuñes 2013 and references therein). While those colonizing species that can establish a foot-hold may be able to adapt to these novel interactions over time (Kaweki 2008, Knope & Scales 2013, Hamilton et al. 2015), early generations will likely display symptoms of living in suboptimal conditions that will affect their fitness and potentially limit their further expansion into the new ecosystem.

Despite the difficulties faced by a colonizing species, pockets of habitat which replicate some of the conditions of its historic ecosystem may exist within the colonized ecosystem. These pockets of habitat can be thought of as analogues to the historic ecosystem of the colonizing species. Thus, we adopt the terms “habitat analogue” and “analogous habitat” from the urban and reconciliation ecology literature (*sensu* Lundholm & Richardson 2010). Habitat analogues have received some attention as artificial habitats found in highly altered ecosystems that replicate conditions experienced by species in their native ecosystems (Lundholm & Richardson 2010 and references therein). These habitats range from quarries (Tropek & Konvička 2008, Tropek et al. 2010) to urban rubble (Grant 2006) and often provide habitat and refuge for species that

could not otherwise thrive in the surrounding ecosystem (Chester & Robson 2013, Lundholm & Richardson 2010). While the terms habitat analogue and analogous habitat have predominantly been used to refer to those habitats found within highly altered ecosystems, the terminology is directly applicable to patches of habitat within natural, but suboptimal, colonized ecosystems that more closely resemble the historic ecosystem of the colonizer. Whether natural or anthropogenic, analogous habitats and other refuges may provide benefits such as a more favorable thermal environment (Wilson et al. 2015, Mosedale et al. 2016), predation refuge (Dumont et al. 2011), and higher quality foraging. Any of these benefits could help a species persist or expand more rapidly into an otherwise suboptimal ecosystem. Thus, these habitat analogues have the potential to play a crucial role in current and future range shifts. However, the impact of analogous habitats and other refuges on range shifting species within colonized ecosystems is relatively understudied (but see Wilson et al. 2015).

The mangrove tree crab *Aratus pisonii* offers an ideal opportunity to examine the impacts of both a colonized ecosystem and a potential analogous habitat on a range shifting species. This arboreal crab is historically associated with Neotropical mangrove forests dominated by the red mangrove *Rhizophora mangle* (Wilson 1989). However, its climate-mediated northward range expansion has recently outpaced that of the mangrove ecosystem resulting in the colonization of salt marshes in the southeastern United States (Riley et al. 2014a). The salt marsh, which is dominated by the grass *Spartina alterniflora*, differs greatly from the mangrove forests where *A. pisonii* has historically been found. The mangrove provides a shaded habitat with tall vertical structure and easy access to the primary food source of *A. pisonii*, *R. mangle* leaves (Beever et al. 1979,

López & Conde 2013), which are absent in the salt marsh. Thus, *A. pisonii* in the salt marsh find themselves in an ecosystem which differs greatly in structure and foraging opportunities from that to which they are adapted. As a result, *A. pisonii* in the salt marsh display smaller body sizes, smaller clutch sizes, and lower larval quality than conspecifics in the mangrove (Riley & Griffen 2017). Thus, it appears that compared to the historic mangrove, the salt marsh is a suboptimal habitat for *A. pisonii*. However, *A. pisonii* is also found on the anthropogenic habitat of docks within the salt marsh.

Analogous habitats confer benefits on a species by being in some way similar to its historic ecosystem. Docks may fit this criterion within the salt marsh as they provide *A. pisonii* with a shaded habitat and vertical structure more similar to the historic mangrove as well as easy access to food in the form of abundant fouling communities. While mangrove leaves are not available in the dock habitat, animal material, which is abundant on docks in the form of fouling communities, is a high-quality food source (Riley et al. 2014b) that is preferred by *A. pisonii* over mangrove leaves (Erickson et al. 2008). Easy access to a high-quality food source could be a boon to *A. pisonii* as the quantity and quality of diet play crucial roles in the energetics and life history of an individual (Wen et al. 2006, Charron et al. 2015). The shaded habitat provided by the dock itself, which is similar to the shade provided by a mangrove canopy, may be an additional benefit as the thermal habitat experienced by an organism has a direct impact on its physiology and life history (Leffler 1972, Huey 1991), especially when warmer than optimal (Gillooly et al. 2001). Thus, the structure, food, and shade provided by docks may allow them to provide improved habitat for *A. pisonii* within the suboptimal salt marsh. The use of anthropogenic structures to provide favorable habitat for species

experiencing adverse effects of climate change has been proposed (Shoo et al. 2011) and implemented (Mitchell et al. 2008) as an aspect of adaptive management (Heller and Zavaleta 2009). However, these structures have always been designed to counteract negative impacts experienced by species in either their historic or highly degraded ecosystems. Unlike the use of shade-cloth shelters (Mitchell et al. 2008) and artificial burrows (Souter et al. 2004), docks represent an anthropogenic habitat found in a colonized natural ecosystem that was not intended to improve habitat conditions.

We examine the impact of the salt marsh and dock habitats on ecological and life history traits of *A. pisonii* that influence both individual performance and the ability of this species to persist and expand into the salt marsh. This includes aspects of behavior related to diet and energy storage, thermal conditions experienced by *A. pisonii*, and an exploration of dietary intake and quality in each habitat. We compare individuals from the colonized habitats (salt marsh and dock) to each other and to a baseline of conspecifics from the historic mangrove ecosystem. We test the overarching hypothesis that in each aspect, *A. pisonii* found on docks within the salt marsh will be more similar to conspecifics in the historic mangrove than to those in the surrounding salt marsh.

3.3 Methods

3.3.1 Study Species

Aratus pisonii is a mangrove associated crab found throughout the Neotropics (Rathbun 1918, Warner 1967). This largely arboreal semi-terrestrial crab has an ecology that is closely tied to the mangrove trees themselves (Warner 1967, Beever et al. 1979). In fact, while it will feed opportunistically on high-quality animal material (Beever et al.

1979, Erickson et al. 2008), its primary food source is fresh mangrove leaves, specifically from the red mangrove *R. mangle* (Beever et al. 1979, López & Conde 2013). Individuals maintain strong site fidelity to individual trees, a behavior lost in the salt marsh, from which they tend to move only a short distance (Cannizzo & Griffen 2016). Despite this fidelity, this crab is not aggressively territorial, it is not uncommon to see numerous individuals in close proximity, and the species maintains a size and sex-based social hierarchy largely through ritualistic displays (Warner 1970). Further, this species is largely terrestrial, returning to the water only to wet its gills and release larvae, and even exhibits a characteristic climbing behavior to avoid aquatic predators when the tide rises (Warner 1967, Wilson 1989).

3.3.2 Site Description

We examined *A. pisonii* in mangrove forests in the vicinity of Fort Pierce, Florida, while individuals in the salt marsh and dock habitats were found in the vicinity of Saint Augustine, Florida (Fig. 3.1; Table A.1). The mangrove sites are within the historic range of *A. pisonii* (Rathbun 1918, Warner 1967) while salt marsh and dock sites represent habitats within the recently colonized region (Riley et al. 2014a). The sites chosen were selected as they are representative of their respective habitat type. Studied salt marsh sites were always at least 0.75 km from the nearest dock to prevent the possibility of examining crabs that have access to the dock habitat. While two salt marsh sites and one dock site were south of the northernmost mangrove (Fig. 3.1), mangroves are scarce in this salt marsh-dominated ecosystem and tend to exist only in small isolated pockets of individuals. Further, only one site of each habitat is south of the northern-most red mangrove, the species to which the ecology of *A. pisonii* is most closely tied in the

mangrove ecosystem (Warner 1967, Beever et al. 1979). While it was impossible to ensure that there was no movement between the dock and salt marsh for crabs examined on docks, crabs tend to exhibit little movement from a central foraging area (Cannizzo & Griffen 2016). Further, even if there is some movement between the habitats, this would result in a conservative test of our hypotheses by minimizing observed differences.

3.3.3 Behavioral observations

We observed the behavior of individual crabs *in situ*. In each habitat, we collected groups of five adult *A. pisonii* by hand and determined the sex and carapace width (to the nearest 0.1mm) of each individual. The groups of crabs were made up of the first five individuals that we encountered and could capture and were drawn from all accessible habitat. We then painted the carapace of each crab an identifying color with nail polish to aid in identification and visibility. Preliminary experiments determined that painting the carapaces of crabs did not alter their behavior or thermal properties. Following a short period of observation to ensure normal behavior, we released the crabs onto a single tree within 10 m of the collection tree of all individuals (mangrove), onto separate *S. alterniflora* stalks within 10 m of the area of collection (salt marsh), or onto the same piling (dock) of the dock where all individuals were captured. Releasing crabs near their capture location allowed for observation while also ensuring as near a natural distribution of crabs as possible. To avoid immediate retreat into holes, release in the salt marsh occurred during the rising tide when the crabs had no access to the sediment.

In all habitats, *A. pisonii* climbs structure as the tide rises to remain out of the water and will even leave occupied shelter to do so (pers. obs.). Thus, we observed crabs

in the mangrove and salt marsh habitats from the time they lost access to the sediment until the receding tide once again allowed access to the sediment (~6h depending on site and day). In contrast, in the dock habitat crabs generally lack access to the sediment throughout the tidal cycle. To obtain an observational period similar to that of the other habitats, we therefore observed crabs on docks from three hours before slack high tide until three hours after slack high tide. We watched crabs from a distance using binoculars to avoid impacting their behavior and monitored the individuals continuously throughout the observational period. The observational location was chosen to maximize visibility and the observer was free to move if increased visibility was necessary. Behavior was recorded every five minutes and at every change in behavior within those five minute intervals as one of four categories: feeding, sitting, moving, or not-visible (Table 3.1). Each group of five crabs was only observed for behavior once and only one group of crabs was observed on any given day. All observations occurred from May through August.

We separated the observations into ebb and flood tidal periods to examine differences in foraging behavior as crabs gained or lost access to food sources on the sediment and wet habitat structure. To avoid biasing the data with crabs that were not visible for long periods, we also removed data from individuals that were not visible for more than 66% of the tidal period. This correction resulted in the observation of 38, 55, and 39 individuals during flood tide and 41, 54, and 39 individuals during ebb tide in the mangrove, salt marsh, and dock habitats respectively. Unless otherwise stated, these individual crabs were treated as the replicates for all associated statistical analyses.

To test for the effects of multiple biological and environmental variables on the proportion of time spent feeding during flood or ebb tide, we ran a generalized linear mixed model with a binomial error distribution. We included carapace width, sex, habitat, air temperature, and tide (ebb or flood) as explanatory variables. We also included the individual crab ID as a random factor to account for the multiple observations of individual crabs (ebb and flood tide) and weighted the model by the total time of observation for each individual. Additionally, we explored the proportion of time *A. pisonii* spent moving by employing a similar generalized linear mixed model but with the proportion of time individuals spent moving as the response variable.

3.3.4 Exposure to thermal microhabitats

To explore the thermal conditions experienced by *A. pisonii* in each habitat, we compared the solar exposure they experienced. We did this by recording the position of crabs as in sun or shade during the behavioral observations described above and calculating the proportion of time they spent in the sun. To confirm the inherent assumption that individuals experience higher temperatures while in the sun, we placed HOBO thermal data loggers underneath a dock, and in a nearby salt marsh at the same site attached to a wooden dowel high enough to remain out of the water. These loggers simultaneously gathered temperature data every minute from noon on 8-Sep-2016 to noon on 11-Sep-2016. The logger data was not collected coincident with observations of crabs as it was not intended to measure the exact temperatures crabs experienced but relative differences between temperatures in the sun and shade. While we took advantage of the structural differences between these habitats to obtain data pertaining to temperature exposure while crabs are in the sun (salt marsh logger) and shade (dock

logger), these measures do not necessarily represent the thermal conditions experienced by all crabs in each of the two habitats at all times. Rather, as the dock and mangrove provide shaded canopies and the salt marsh does not, they represent the difference in the thermal conditions most often experienced by the crabs in each habitat.

To further examine the thermal habitat experienced by the observed crabs, we used a FLIR instruments C2 compact thermal imaging camera to take a thermal image of each visible marked crab every 15 minutes throughout the observational period. The days when crabs were observed took place over a wider range of air temperatures, which was measured on site, in the mangrove and salt marsh habitats than on docks. Thus, to avoid the confounding factor of relatively cooler air temperatures in these habitats, only thermal pictures taken on days which had an average air temperature greater than 29^{o}C were examined. This temperature represented the lower bound of air temperatures on days crabs were observed in the dock habitat. Along with the elimination of photographs where no crabs were visible, this resulted in in the analysis of 455, 294, and 289 thermal photos from the salt marsh, mangrove, and dock habitats respectively. We then employed the program FLIR tools to obtain the temperature at the center of the carapace of each crab.

We suspected that the proportion of time crabs spent in both the water and the sun would impact their body temperature so we calculated these values for all individuals for which we had thermal photos. We compared these values between habitats using an ANOVA followed by a Tukey's HSD test for multiple comparisons. Unless otherwise stated, we implemented this statistical method for all subsequent comparisons made between and within habitats.

To explore the factors that influence crab temperature, we averaged the recorded body temperature of individual crabs over the course of an observational period. We expected that the solar radiation experienced by crabs over the course of an observational period (~6h depending on site and day) would impact their body temperature. Thus, to examine the impact of solar exposure on crab temperature, we obtained short and long-wave solar radiation from the NCEP North American Regional Reanalysis (NARR). NARR has a resolution of 32km and calculates solar radiation in 3hr intervals. We obtained the solar radiation at the grid point closest to each site and averaged the sum of the short and long-wave solar radiation over the observational period. This number, in W/m^2 was then multiplied by the number of seconds the crab was observed to spend in the sun to obtain a relative measure of the solar energy experienced over the observational period. This calculated variable will hereafter be referred to as "solar exposure". We then ran a mixed effects linear model with habitat, proportion of time in water, solar exposure, and ambient air temperature as explanatory factors for the averaged crab body temperatures, which were included as the response variable in the model. We also ran a similar model with the average difference between crab body temperature and the ambient air temperature as the response variable. This model allowed us to analyze the ability of crabs in each habitat to maintain a body temperature cooler than ambient and explore the factors that impact this ability. In both models, the continuous explanatory variables were z-scored to facilitate comparison of their relative impacts on the response variable. Due to the site-fidelity behavior of *A. pisonii* (Cannizzo & Griffen 2016), some crabs were photographed on multiple days. Thus, to account for these multiple observations, crab ID was included in the models as a random factor.

These models allowed us to explore the impact of these factors on both crab body temperatures and cooling on the time scale on which the explanatory factors were available and meaningful. Finally, we ran linear regressions to determine if there were relationships between the proportion of time individuals spent in the water and sun as well as the time spent in water and solar exposure.

3.3.5 Diet and energy storage

To examine diet indices and the investment of *A. pisonii* into energy storage, we collected individuals from each habitat during the summers of 2015 and 2016. On each of 9 randomly selected days in each habitat, 15 individual adult *A. pisonii* were collected by hand and immediately placed on dry ice. In the mangrove and salt marsh, we collected these crabs in three groups of five at three distinct tidal periods: just after losing access to the sediment on the flood tide, at slack high tide, and just before regaining access to the sediment on the ebb tide. This resulted in collection times ~3h apart. Due to the constant lack of access to sediment in the dock habitat, we collected crabs three hours before, at, and three hours after slack high tide. As in the behavioral observations, the first five crabs we encountered were collected at each of these tidal periods. This collection regime resulted in a total of 135 crabs from each habitat (45 from each tidal period) which were kept frozen until dissection. No measured indices differed between years and thus data were pooled across years for analysis.

Based on preliminary observations in the laboratory, the gut clearance time of *A. pisonii* is ~3h. Therefore, our collection regime allowed for the analysis of diet when crabs had access to the sediment (collected on the flood tide), when crabs only had access

to unsubmerged habitat (collected at slack high tide), and when crabs had access to recently submerged habitat (collected on the ebb tide). Prior to dissection, we determined the sex and carapace width (to the nearest 0.1mm) of each crab.

We ascertained the gut fullness of each crab to obtain a snap-shot of the quantity of food consumed during each tidal period by removing the gut contents and drying them at 60-70^{o}C to constant weight. We standardized gut fullness by dividing the mass of the gut contents by the volume of the gut ($\mathrm{V} = \mathrm{a}\frac{\sqrt{2}}{12} \times \mathrm{Gut\ width}^3$ where *a* is a correction factor of 0.92 for crabs (Griffen & Mosblack 2011)). We then employed a two-way ANOVA to compare the standardized gut fullness between tidal periods within and between habitats. Due to inclement weather during one observation day in the dock habitat, crabs were collected without regard for tidal period. This lead to only 120 crabs from the dock, 40 per tidal period, being analyzed for gut fullness. As this was the only dissection parameter dependent on time of collection (see below), only gut fullness was impacted by this reduced sample size.

In addition to diet quantity, we explored long-term diet quality by measuring the cardiac stomach of each crab to the nearest 0.1mm and comparing the gut-width:carapace-width ratio between habitats. In crabs, this ratio is a proxy for long-term diet quality with a smaller ratio corresponding to a higher quality diet that likely contains more animal material (Griffen & Mosblack 2011).

To examine the proportional energetic investment into energy storage by conspecifics in each habitat, we separated and dried the primary energy storage organ (hepatopancreas) (Parvathy 1971) and the somatic tissue of each crab. To compare

energetic investment between habitats, we calculated the hepatosomatic index (HSI) of each crab as the ratio of the dry weights of the hepatopancreas and the somatic tissue, which is a common measure of energy stores in crustaceans (Kennish 1997, Sánches-Paz et al. 2007, Griffen et al. 2015, Riley et al. 2014b). However, HSI is dependent on both sex and reproductive stage (ex: a female will have a lower HSI when carrying eggs; Belgrad et al. 2017). Thus, we grouped crabs as male, gravid female, or non-gravid female and compared the HSI of these groups between habitats. Due to a problem in transportation, the legs of crabs from two tidal periods on one day from the mangrove became detached and mixed. This made it impossible to reliably obtain a weight for somatic tissue from these 10 crabs resulting in a reduced sample size of 125 crabs from the mangrove analyzed for HSI. As this was the only parameter that incorporated somatic weight, it did not affect the sample size of any other analysis.

3.3.6 Statement of Animal Rights

All applicable institutional and/or national guidelines for the care and use of animals were followed.

3.4 Results

3.4.1 Demographics

Aratus pisonii in the salt marsh habitat were smaller (CW±SD = 12.97±1.57mm) than conspecifics in the mangrove (17.95±3.12mm) and dock (17.83±2.09mm) habitats (ANOVA, F_2=314.9, $p<0.001$; Tukey's HSD, $p<0.001$, Fig. A.1). However, individuals found in the dock habitat did not differ in size from conspecifics in the mangrove (Tukey's HSD, $p=0.850$, Fig. A.1).

3.4.2 Behavioral Observations

For the results presented below, "estim." refers to the parameter estimate for the statistical model being reported. The proportion of time *A. pisonii* spent feeding was lower in the mangrove (Prop. time±SD = 0.152±0.139) than the dock (0.190±0.162; GLM, estim.= -0.754, z=-3.01, p=0.003) and salt marsh habitats (0.189±0.190; GLM, estim.= 0.792, z=3.28, p=0.006) but did not differ between the dock and salt marsh (GLM, estim.= -0.218, z=-0.94, p=0.349). Time spent feeding was not affected by carapace width or sex (GLM, estim.= -0.042, z=-0.99, p=0.326; estim.= 0.382, z=1.87, p=0.062 respectively), but was influenced by a number of environmental factors. Feeding decreased as air temperature increased (GLM, estim.= -0.135, z=-6.90, p<0.001), but increased as the tide fell and foraging on recently submerged structure became possible (GLM, estim.= 1.460, z=43.28, p<0.001). Time spent feeding also differed within habitats and was contingent on the tidal period (Two-Way ANOVA, Habitat*Tide, F_2=8.664, p<0.001; Tukey's HSD, p<0.05, Fig. 3.2). Additionally, foraging depended on interactions between the tide and habitat. After slack tide, crabs in the salt marsh exhibited a 1.4-fold greater increase in feeding than crabs on docks (GLM, estim.= 3.975, z=3.63, p<0.001) and a 5.7-fold greater increase than conspecifics in the mangrove (GLM, estim.=4.655, z=4.76, p<0.001) while the increase in feeding during this period (ebb tide) did not differ between the mangrove and dock habitats (GLM, estim.=-0.755, z=0.66, p=0.507). As with tidal period, temperature impacted feeding differently between habitats. Individuals in the dock habitat increased the proportion of time they fed as temperatures rose (GLM, estim.=0.526, z=8.74, p<0.001 Fig. A.2,) while the opposite was observed in both the mangrove (GLM, estim.=-0.525, z=-8.73 p<0.001) and salt

marsh (GLM, estim.=-0.330, z=-2.22 p<0.001) driving the overall negative impact of temperature on time spent feeding. Additionally, the interaction between temperature and habitat revealed that this reduction in feeding with increased temperature was greater in the mangrove than in the salt marsh (GLM, estim=0.195, z=3.24 p=0.002).

Movement patterns were similar to those seen in feeding as the proportion of time *A. pisonii* spent moving was not contingent upon individual size or sex (GLM, estim.= -0.021, z=-0.74, p=0.458; estim.= 0.148, z=1.003 p=0.316 respectively), but was impacted by environmental factors. However, in contrast to feeding, movement decreased during ebb tide (GLM, estim.= -0.206, z=-4.46 p<0.001) and increased with air temperature (GLM, estim.= 0.0433, z=2.25, p=0.024). Additionally, individuals in the mangrove spent a greater proportion of time moving (Prop. time±SD = 0.116±0.018) than conspecifics in the salt marsh (0.032±0.037; GLM, estim.= 1.698, z=9.73, p<0.001) and dock habitats (0.040±0.040; GLM, estim.= 1.322, z=7.44 p<0.001). However, movement did not differ between the salt marsh and dock habitats (GLM, estim.= -0.293, z=-1.73 p=0.084). The interaction between movement and tide revealed that individuals in the dock habitat increased the proportion of time they moved after slack tide (ebb tide) as opposed to the decrease in movement in both the mangrove (GLM, estim.=-3.658, z=2.49, p=0.021) and salt marsh (GLM, estim.=-6.110, z=-3.44, p<0.001) which drove the overall negative trend of reduced movement after slack tide. However, the decrease in movement during ebb tide did not differ between the mangrove and salt marsh (GLM, estim.=-2.433, z=-1.78, p=0.076).

3.4.3 Exposure to thermal micro-habitats

The thermal conditions experienced by *A. pisonii* differed greatly between habitats. Individuals observed in the dock and mangrove habitats spent a similar amount of time in the shade (Tukey's HSD, p=0.938, Fig. 3.3a) and more than 18-fold less time in the sun than conspecifics in the salt marsh (ANOVA, F_2=110.5 p<0.001; Tukey HSD, p<0.001, Fig. 3.3a). This likely resulted in individuals in the mangrove and dock habitats experiencing a cooler microhabitat, as temperatures recorded during the day were as much as 10ºC cooler in the shade of a dock than in the nearby salt marsh (Fig. 3.3b). We confirmed this conclusion through the analysis of crab body temperatures obtained from the thermal photographs.

Habitat played an important role in determining crab body temperature. Crabs in the salt marsh had higher body temperatures than those found in the dock and mangrove habitats (LMER, estim. = -1.1272, t_{98}=-2.473 p = 0.0151; estim. = -1.8366, t_{90}=-3.63, p <0.001 respectively; Fig. 3.4a). These individuals were also less able to maintain a body temperature cooler than the ambient than conspecifics in the dock and mangrove habitats (LMER, estim. = -1.2825, t_{106}=-3.01 p = 0.0033; estim. = -2.004, t_{96}=-4.21 p <0.001 respectively; Fig. 3.4b). Additionally, compared to conspecifics in the mangrove, crabs in the dock habitat had a higher body temperature (LMER, estim. = -0.7095, t_{64}=-2.427 p = 0.0181) and were and less able to maintain a body temperature cooler than the ambient (LMER, estim. = -0.7180, t_{68}=-2.56 p = 0.0126). The temperature of crabs also increased with ambient air temperature (LMER, estim. = 0.9765, t_{99}=8.99 p <0.001) and decreased as a crab spent a greater proportion of its time in the water (LMER, estim. = -2.4725, t_{98}=-2.21 p = 0.0295). However, the amount of solar exposure a crab experienced did not

have a significant impact on its body temperature (LMER, estim. = -0.3378, t_{99}=-1.64 p = 0.1036). In addition, crabs maintained body temperatures progressively cooler than ambient as the ambient temperature increased (LMER, estim. = -0.7839, t_{105}=-7.51 p <0.001), as solar exposure increased (LMER, estim. = -0.4262, t_{105}=-2.23 p = 0.02813), and as crabs spent more time in the water (LMER, estim. = -2.6752, t_{104}=-2.47 p = 0.0152). Further, crabs in the salt marsh spent a greater proportion of their time in the water than conspecifics in the mangrove (ANOVA, F_2=8.813, p<0.001; Tukey HSD, p<0.001; Fig. A.3) and dock habitats (Tukey HSD, p=0.0087; Fig. A.3) which did not differ in this regard (Tukey HSD, p=0.0732; Fig. A.3). This is of note as there was a positive relationship between the time a crab spent in the water and both the time it spent in the sun and its solar exposure (LM, t_{103}=2.198, p=0.030; t_{103}=1.996, p=0.048 respectively).

3.4.4 Diet and energy storage

The gut fullness of *A. pisonii* differed dependent on both habitat (Two-Way ANOVA, F_2=14.75, p<0.001, Fig. A.4) and tidal period (Two-Way ANOVA, F_2=15.38, p<0.001). In particular, the interaction of habitat and tidal period (Two-Way ANOVA, F4=5.18, p<0.001) suggests that gut fullness was dependent on a combination of these variables. When analyzed by habitat it is clear that *A. pisonii* were able to maintain a consistent gut fullness throughout the tidal cycle in both the mangrove (Tukey HSD, p>0.50; Fig. 3.5) and dock habitats (Tukey HSD p>0.50; Fig. 3.5). However, despite an overall higher gut fullness (Tukey HSD, p<0.001, Fig. A.4), crabs in the salt marsh were unable to maintain a full gut, and thus were likely unable to obtain sufficient food, during the time when the rising tide restricts access to food found on the sediment or deposited

by water on structure (Tukey HSD, $p<0.001$; Fig. 3.5). During other times in the tidal cycle, however, crabs in the salt marsh maintained a higher gut fullness than conspecifics in the mangrove and dock habitats (Two-Way ANOVA, $F_4=5.18$, $p<0.001$; Tukey HSD, $p<0.01$; Fig. 3.5). In addition to unreliable foraging, *A. pisonii* in the salt marsh had a higher gut-width:carapace-width ratio, indicating a lower quality long-term diet, than conspecifics in either the historic mangrove or dock habitat, where diet quality was highest (ANOVA, $F_2=20.52$, $p<0.001$; Tukey's HSD, $p<0.05$, Fig. 3.6).

Proportional energetic investment into energy storage (HSI) was highest in the mangrove for both males (ANOVA, $F_2=23.27$, $p<0.001$; Tukey HSD, $p<0.001$) and gravid females (ANOVA, $F_2=29.24$, $p<0.001$; Tukey HSD, $p<0.001$, Fig. 3.7). Energy storage was also greater in gravid females in the salt marsh than on docks (Tukey HSD, $p<0.001$, Fig. 3.7), but did not differ between these two habitats in males (Tukey HSD, $p=0.065$, Fig. 3.7). In non-gravid females, energy storage was lowest in the dock habitat (ANOVA, $F_2=36.13$, $p<0.001$; Tukey HSD, $p<0.001$, Fig. 3.7) but did not differ between the mangrove and salt marsh (Tukey HSD, $p=0.060$, Fig. 3.7).

3.5 Discussion

Compared to the historic mangrove, the salt marsh proved to be a suboptimal habitat for *A. pisonii* in every measured aspect of this study. Further, this study suggests that the role of the dock habitat in providing improved conditions for *A. pisonii* within the colonized salt marsh ecosystem is mixed. Yet, while docks do not provide improved conditions in every way, they do appear to provide improvements for a number of important aspects of this crab's ecology and physiology. One important benefit conferred

by docks is larger body size. While there is as yet no reliable way to age these crabs (Hartnoll 2001, Vogt 2012), and thus no way to determine to relative impacts of age and growth-rate, a larger body size is often beneficial. For *A. pisonii*, larger size confers benefits through size-specific dominance hierarchies (Warner 1970) and increased reproductive output (Riley & Griffen 2017), which in turn benefits the population. Thus, greater size is an example of an individual benefit provided by an analogous habitat that may have cascading benefits for a range shifting species.

Understanding how analogous habitats confer general benefits, such as larger size, requires an understanding of the mechanisms that lead to those benefits. This can be explored through the examination of the precise ways in which an analogous habitat provides improved conditions. For example, the quantity and quality of an individual's diet has a direct impact on several aspects of its ecology and life history including growth (Buck et al 2003, Griffen et al 2008), offspring quantity and quality (Millamena & Quinitio 2000, Green et al. 2014), and bioenergetics (Riley et al. 2014b, Charron et al. 2015). Thus, an improved diet may itself be the mechanism behind other benefits including increased size. Docks clearly provide improved diet and foraging conditions to *A. pisonii* through more continuous access to a higher quality diet than elsewhere in the salt marsh. However, the high gut fullness displayed by crabs in the salt marsh when the sediment is accessible and during ebb tide suggests that they exhibit compensatory feeding through increased consumption when food is available. While compensatory feeding is common among individuals faced with poor diets, it is not always effective (Cruz-Rivera & Hay 2000) and may be hindered by irregular access to food in the salt marsh. In addition to regular access to food, docks provide abundant animal protein, a

high-quality food (Riley et al. 2014b), in the form of high-density fouling communities. We regularly observed *A. pisonii* feeding on fouling organisms suggesting that animal material plays an important role in the improved diet quality of these crabs.

Similarly to diet, the thermal conditions experienced by an organism greatly impact its physiology and life history (Leffler 1972, Huey 1991). Thus, improved thermal conditions are a potential mechanism that could lead to other benefits including larger size (Leffler 1972, Huey 1991). For *A. pisonii*, docks provide a shaded thermal refuge which allows crabs to maintain a body temperature that is lower, and lower than ambient to a greater extent, than conspecifics elsewhere in the salt marsh. In fact, the extensive use of shaded areas of the dock and mangrove habitats suggests that shaded areas are preferred by *A. pisonii* and the excessive time conspecifics from the salt marsh spend in the sun is likely a result of the habitat structure, not preference. The use of thermally sheltered habitats in such areas where preferred thermal conditions are not readily available is a primary way in which species may address regional climatic shifts (Williams et al. 2008). While we focused on the ability of docks to provide crabs a cooler habitat during summer months, the ability of an analogous habitat to provide a warmer microhabitat in winter months could also be vital to a range shifting species.

Despite the cooler conditions provided by docks, the thermal differences observed between habitats were less than the disparity in time spent in the sun would suggest. One possibility is that crabs in the open-structured salt marsh experience greater convective cooling due to increased wind exposure (Ortega et al. 2017). However, our results suggest that the lower than expected body temperature of crabs in the salt marsh is more likely a result of differences in thermoregulatory behavior. Crabs in the salt marsh appear

to thermoregulate by dipping in water to cool themselves after extended time in the sun, a conclusion supported by the positive relationship between time in water and solar exposure. Indeed, a comparison of the z-scored model estimates suggests that the time crabs spend in the water has the largest impact on both their body temperature and their ability to maintain a body temperature cooler than the ambient air. Additionally, dipping in water could have an additional cooling effect even after the crab emerges via evaporative cooling (Eshky et al. 1995), which could also be further enhanced by increased wind exposure. Indeed, in combination with the result that crabs spend more time in the water when experiencing greater solar exposure, it is possible that this could explain the unexpected negative effect of solar exposure on the difference between crab body temperature and the ambient air temperature. Thus, while exposure to the sun surely has an acute warming impact on crabs, its statistical impact is likely overpowered by the impact of cooling with water.

The change in thermoregulatory behavior in the salt marsh suggests another way in which analogous habitats may provide improved conditions in colonized ecosystems: by allowing individuals to avoid potentially costly changes in behavior. While behavioral changes often provide the first response to altered environments (Gross et al. 2010, Sih et al. 2011, Wong & Candolin 2015), they can lead to costly ecological trade-offs. For *A. pisonii*, the need to thermoregulate may require crabs to temporarily abandon forage or shelter to move to water where they are likely exposed to higher predation (Warner 1967, Wilson 1989). In fact, previous work suggested that predation on large individuals may be lower in the mangrove than the salt marsh which may contribute to the size disparity between the two habitats (Riley & Griffen 2017). It is possible that the risk of predation

for large individuals is also lower on docks, particularly considering the low occurrence of small individuals (Fig A.1), further contributing to the larger size of individuals found there. However, while docks may allow *A. pisonii* to avoid risky thermoregulatory behavior, crabs found there exhibit foraging behavior that differs from crabs in the mangrove and is similar to conspecifics elsewhere in the salt marsh. Crabs in the dock and salt marsh habitats increase their feeding as the tide falls suggesting they feed heavily on food that is either deposited on structure or submerged at high tide. This differs from conspecifics in the historic mangrove which feed on continuously accessible mangrove leaves. Like dipping in water to thermoregulate, following receding water to feed may increase the risk of predation by aquatic predators (Warner 1967, Wilson 1989). Thus, the ability of docks to allow *A. pisonii* to avoid potentially dangerous behavioral changes is mixed.

Foraging behavior is not the only way docks fail to provide improved conditions for *A. pisonii*. In particular, the proportion of energy stored by crabs in the three habitats differed in unexpected ways. While the investment into energy storage (HSI) was lower in the salt marsh than the historic mangrove habitat, it was lower still in crabs found on docks. This is particularly perplexing when considering the larger size and improved diet of crabs on docks. It is possible that the differences in diet observed between habitats play a role in the ability of *A. pisonii* to convert consumed energy into stored energy. Alternatively, some unknown energetic expense or trade-off in the dock habitat may lead to a decrease in energy storage. In any event, the energy storage of *A. pisonii* warrants further study and suggests that crabs on the docks likely have different patterns of energy use than those in the surrounding salt marsh ecosystem. Given the metabolic costs for

crabs of storing lipids in the hepatopancreas (Griffen 2017), the lower HSI seen in crabs on the docks could be beneficial for individuals and may reflect improved energetic efficiency for crabs using this habitat type.

While docks appear to provide several important benefits to *A. pisonii* in the colonized salt marsh ecosystem, their role as an analogue to the mangrove is clearly mixed. Yet, what docks do represent is a relatively understudied aspect of range shift ecology: the role of anthropogenic habitat analogues in providing improved conditions within suboptimal colonized natural ecosystems. However, a number of studies have proposed implementing artificial habitats, or habitat modification, to minimize the exposure of vulnerable species to stressful changing conditions in their historic ecosystems (Williams et al. 2008, Shoo et al. 2011). Such proposals have included installing microhabitat refuges and sprinklers for amphibians (Shoo et al. 2011), artificial breeding structures (Shoo et al. 2011), shade cloths (Mitchell et al. 2008), and general habitat restoration using artificial structures such as burrows (Souter et al. 2004) and formed concrete (Webb & Shine 2000). However, the use of anthropogenic habitats in natural ecosystems that a species has never before inhabited has garnered little discussion.

The construction of artificial habitats in unsuitable ecosystems to help/encourage range shifts has received some discussion as a facet of adaptive management strategies (Hoegh-Guldberg et al. 2008). Additionally, there has been a robust discussion of the use of corridors to aid species in their climate-induced range shifts (Hannah 2001, Krosby et al. 2010). In fact, increasing ecological connectivity through cities and other unfavorable habitats to encourage the movement of species between natural areas has been identified

as critical to the ability of many species to persist in the face of changing climatic conditions (Krosby et al. 2010, Williams et al. 2014). Such discussions tend to focus on creating or preserving natural corridors between natural areas (Hannah 2001, Krosby et al. 2010). In contrast, anthropogenic habitat analogues may increase, rather than impede, the success and rate of range shifts. While there has been some exploration of green roofs (Williams et al. 2014 and references therein), gardens (Goddard et al. 2010), street side vegetation (Swan et al. 2011), and other anthropogenic "stepping-stone" refuges (Gledhill et al. 2008, Santoul et al. 2009, Chester & Robson 2013) in facilitating movement through cities and other unfavorable habitat, this work has largely focused on biodiversity conservation and movement between habitable areas as opposed to range shifts (but see Grant 2006). Yet, anthropogenic structures which were not specifically designed as habitat could increase the permeability of the habitat matrix during range shifts by providing more favorable habitat than the surrounding ecosystem. Even if anthropogenic habitat analogues do not increase the rate of a range shift, their ability to provide improved conditions could prove vital to the success of range shifting species in colonized ecosystems.

As climate change continues to force or encourage species to colonize new ecosystems, it will be increasingly important to understand how these shifting species are impacted by habitats with which they have no ecological or evolutionary experience. The role of anthropogenic habitats as habitat analogues may play a crucial role in the outcome of range shifts. Thus, the existence of anthropogenic habitat analogues should be included in analyses of the vulnerability of species to climate change (see Williams et al. 2008 for a framework for such an analysis). Ultimately, the individual benefits conferred by docks

suggest that they likely have a positive impact on the population of *A. pisonii* in the salt marsh. Therefore, this study suggests that anthropogenic habitats have the potential to play an important role in providing improved conditions to range shifting species experiencing suboptimal conditions in colonized ecosystems. While no habitat analogue is likely to ameliorate all negative novel interactions experienced by range shifting species, amelioration of even a small number of negative impacts will likely be beneficial to both individuals and populations. If the patterns that we document are general across systems, then anthropogenic habitats may play an important facilitative role in the range shifts of species with continued climate change.

3.6 Acknowledgments

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3.7 Tables

Table 3.1. Ethogram describing the behavioral categories assigned while observing *A. pisonii*

Behavior	Description
Feeding	The crab is observed actively moving its claws from a food item or substrate to its mouth.
Moving	The crab is actively moving along a substrate and not feeding. Other energy expending non-feeding activities, such as ritual aggression, were also classified under moving as they represent an expenditure of energy. However, these activities were rare and short lived.
Sitting	The crab is not actively moving, feeding, or participating in any activity.
Not-visible	The crab is not visible to the observer.

3.8 Figures

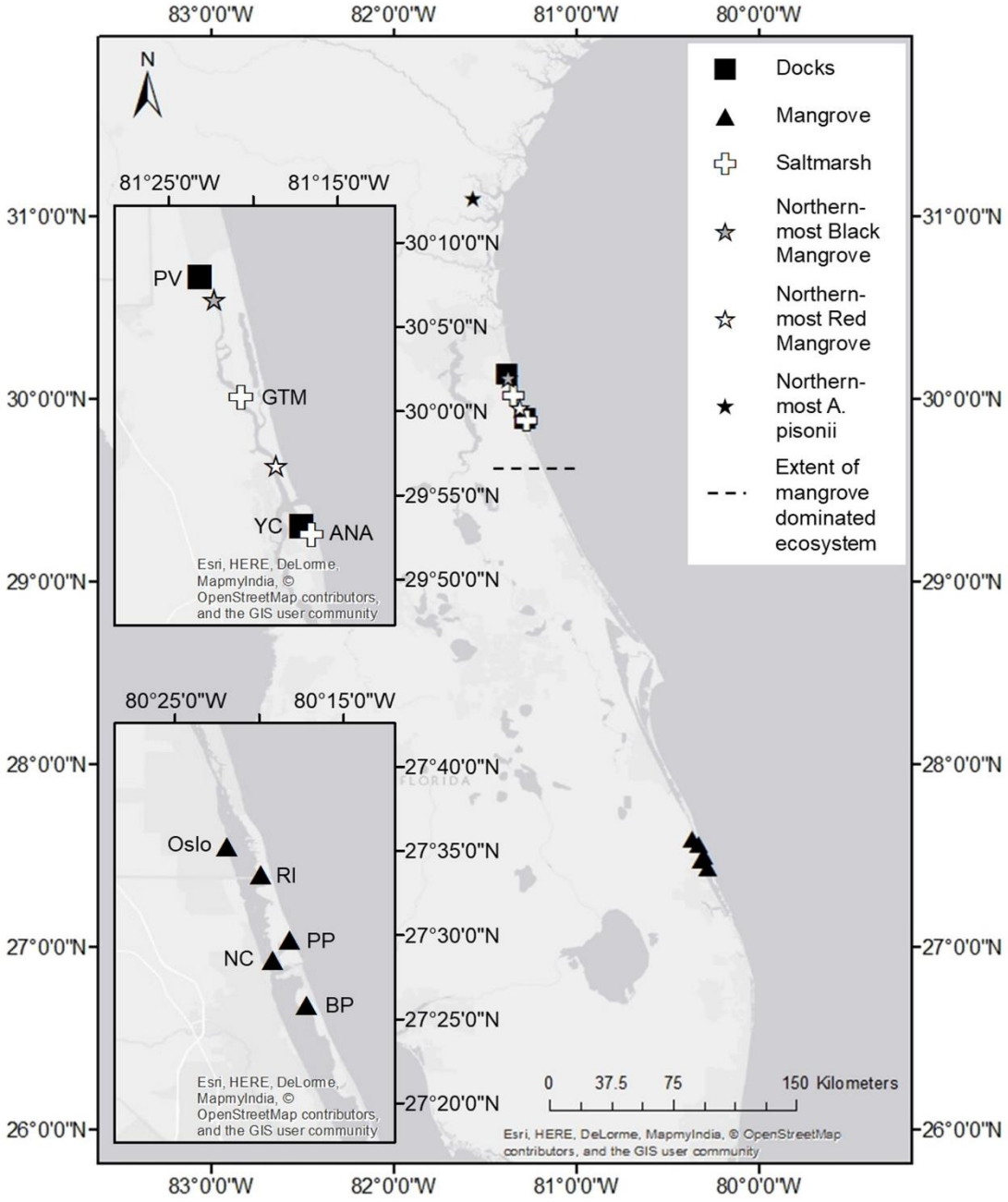

Figure 3.1. Map of the location of study sites, northern-most *A. pisonii* (Riley et al. 2014a), and northern-most black (*Avicennia germinans*) and red (*Rhizophora mangle*) mangroves (Williams et al. 2014). The map also displays a point delineated as the extent of the mangrove dominated ecosystem. While the transition from mangrove to saltmarsh exists as a mosaic-like ecotone, this location represents an area with roughly 50:50 mangrove:saltmarsh coverage (Rodriguez et al. 2016; IC Feller pers. com.). North of this line, mangroves can still be found but are progressively more isolated and exist as individuals or small patches within a saltmarsh dominated ecosystem.

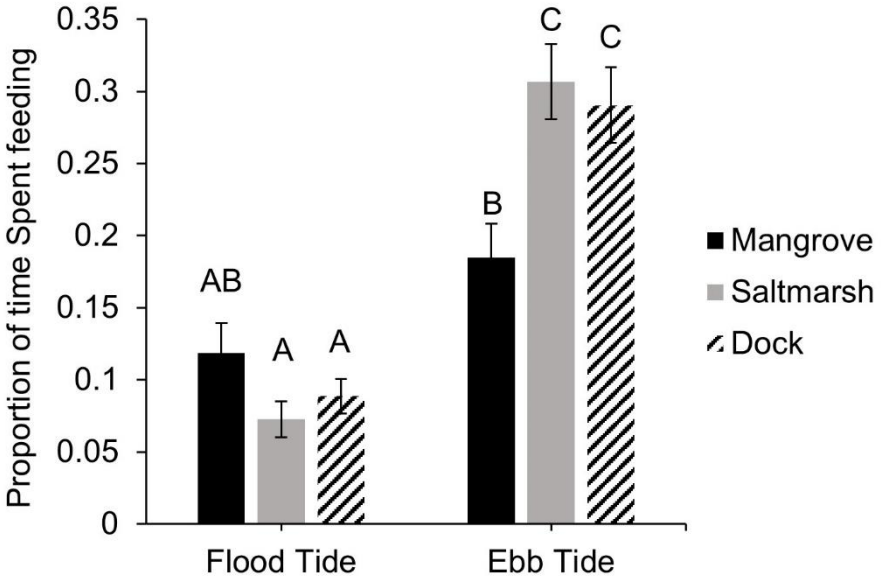

Figure 3.2. The proportion of time spent feeding ± SE by *A. pisonii* in the mangrove, saltmarsh, and dock habitats before and after slack-high tide. Groups that are significantly different are denoted by different letters.

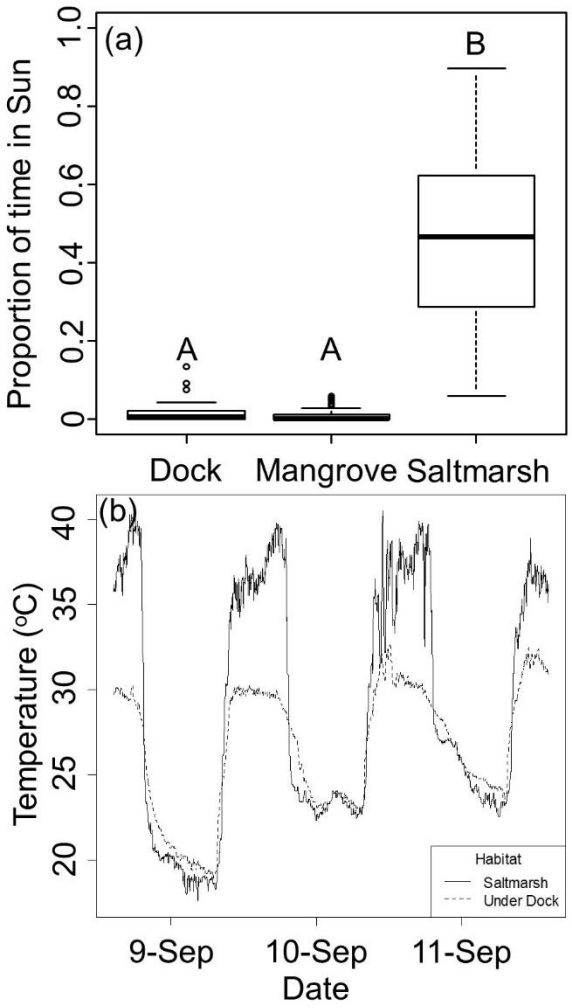

Figure 3.3. (a) Boxplots comparing the proportion of time spent in sun by *A. pisonii* between the three habitats. Groups that are significantly different are denoted by different letters. In each boxplot, and in all other boxplots represented in this paper, the median is represented by a heavy line, the box represents the upper and lower quartiles, while the whiskers represent 95% of the data and circles show outliers. (b) Thermal logger data of loggers placed in the shade under a dock (dashed line) and in the open in the saltmarsh (solid line) from 8-Sep-2016 to 11-Sep-2016.

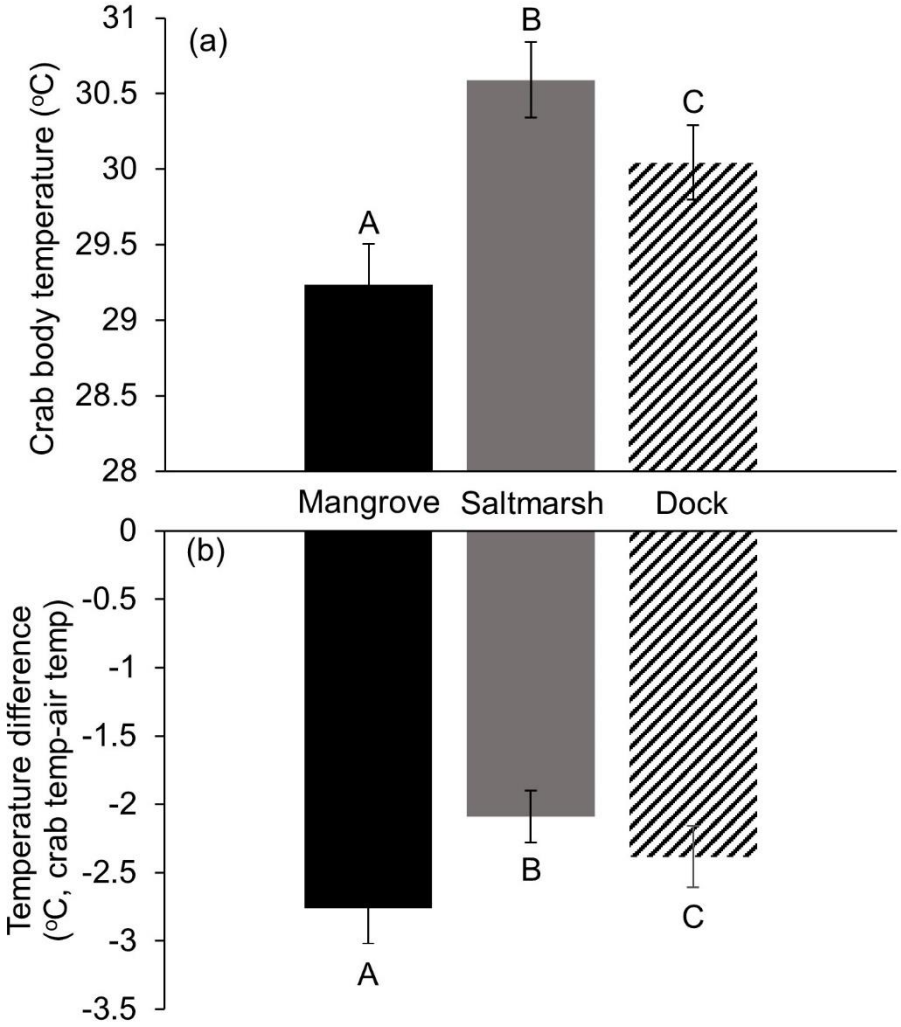

Figure 3.4. (a) Average body temperature ± SE of crabs in each habitat. Groups that are significantly different are denoted by different letters. (b) Differences between average crab body temperature and ambient air temperature ± SE in each habitat. Groups that are significantly different are denoted by different letters.

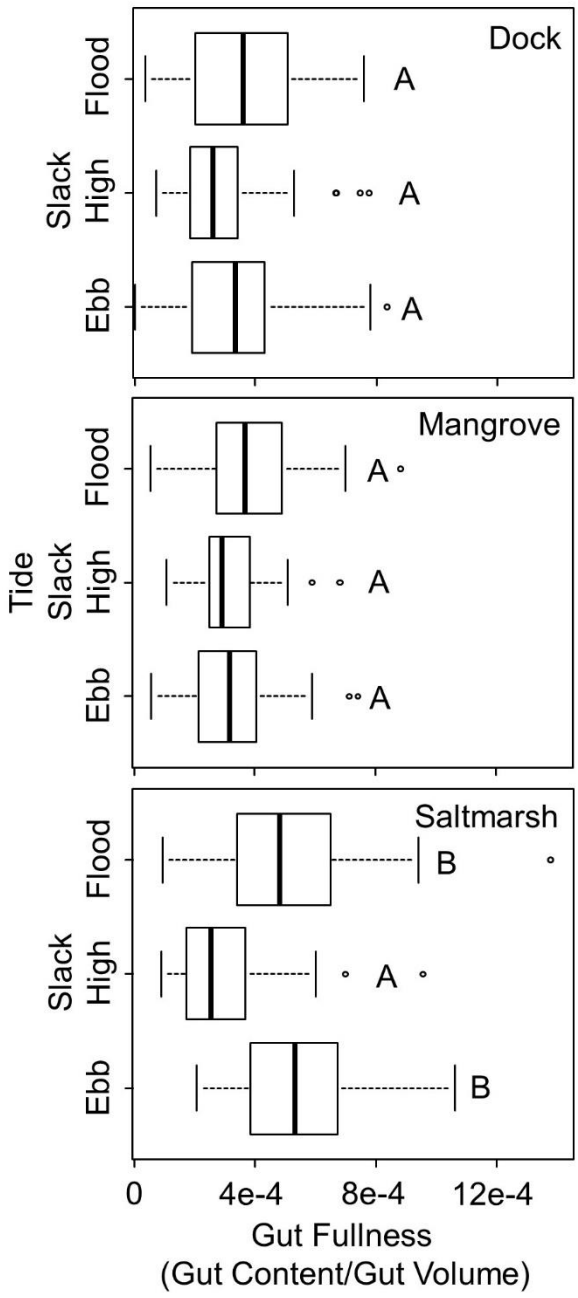

Figure 3.5. Boxplots showing the gut fullness of *A. pisonii* by tidal period in the mangrove, saltmarsh, and dock habitats. Groups that are significantly different are denoted by different letters.

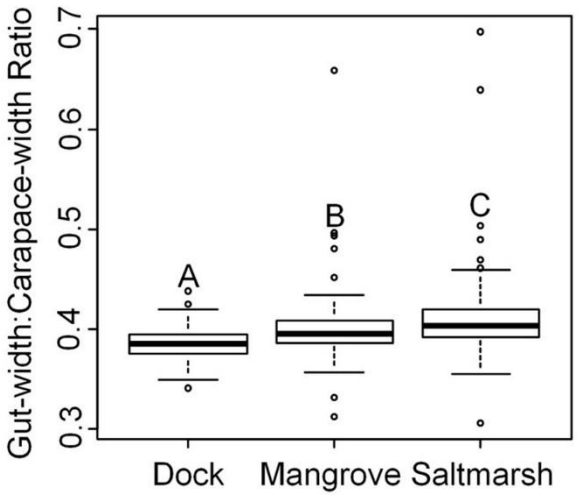

Figure 3.6. Boxplots comparing the gut-width:carpace-width ratios of *A. pisonii* between the mangrove, saltmarsh, and dock habitats. Groups that are significantly different are denoted by different letters. A lower gut-width:carapace-width ratio suggests a relatively higher proportion of animal material in the long-term diet of the individual.

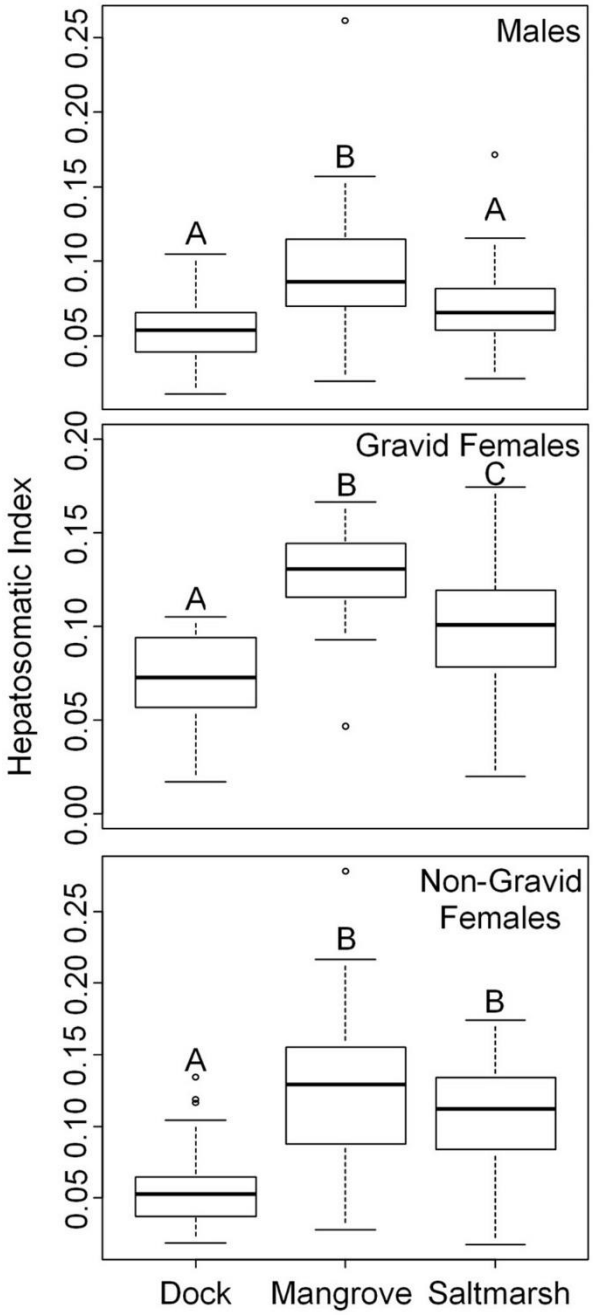

Figure 3.7. Boxplots comparing the investment in long-term energy storage, calculated as hepatosomatic index, of male, gravid female, and non-gravid female *A. pisonii* between the three habitats. Groups that are significantly different are denoted by different letters.

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CHAPTER 4

AN ARTIFICIAL HABITAT INCREASES THE REPRODUCTIVE FITNESS OF A RANGE SHIFTING SPECIES WITHIN A NEWLY COLONIZED EOCSYSTEM

4.1 Abstract

When a range shifting species colonizes an ecosystem it has not previously inhabited, it may experience suboptimal conditions that are harmful to its ecology and life history, challenging its ability to continue to persist and expand. Some of these impacts may be partially mitigated by artificial habitat analogues: artificial habitats that more closely resemble the historic ecosystem of a species than the surrounding habitat. If conditions provided by such habitats increase reproductive success compared to individuals in the surrounding suboptimal ecosystem, they could play vital roles in the expansion and persistence of range shifting species. We investigated the reproduction of the mangrove tree crab *Aratus pisonii* in the historic mangrove habitat, the suboptimal colonized salt marsh ecosystem, and on docks within the salt marsh, a habitat analogue to its historic mangrove ecosystem. Conspecifics from the three habitats were assessed for offspring production and quality, as well as measures of maternal investment and egg quality. Crabs found on docks produced more eggs overall, more eggs per investment, and higher quality larvae than conspecifics in the surrounding colonized salt marsh. Yet, crabs in the historic mangrove produced larvae of even higher quality. Mechanistically, egg lipids and fatty acids suggest the different reproductive outcomes result from disparities in the quality of diet-driven maternal investments, particularly key fatty acids. Ultimately, this study suggests that habitat analogues may increase the reproductive fitness of range shifting species and allow them to expand more quickly into, and better persist in, colonized ecosystems.

4.2 Introduction

One of the most widespread symptoms of climate change is the ongoing global shift in species distributions (Walther et al. 2002, Sorte et al. 2010, Canning-Clode et al. 2011). In some instances, species shift at different rates than the foundation species of their historic ecosystems (Schweiger et al. 2008). When this occurs, a shifting species may colonize an ecosystem for which it has no ecological or evolutionary experience (Schweiger et al. 2008) and where novel interactions are likely to result in suboptimal conditions (Holt et al. 2005, Keller & Taylor 2008, Riley & Griffen 2017, Cannizzo et al. 2018). While species may be able to survive in such colonized suboptimal ecosystems, their continued spread and persistence may be hindered. As such colonizations are expected to increase (Schweiger et al. 2008, Walther 2010), understanding how habitat effects impact the fitness of species in newly colonized ecosystems is vital to understanding and predicting geographic range shifts.

Reproductive fitness is central to individual and population success. The importance of reproduction is further magnified during range shifts, as propagule pressure is one of the primary determinants of success during colonization and expansion (Colautti et al. 2006, Simberloff 2009). This is particularly true of passively dispersing organisms, as a multitude of high quality offspring will increase dispersal (Chuang & Peterson 2016). Habitat effects can have critical impacts on reproductive potential through a range of environmental and biological factors (Helm et al. 1973, Gardner 2001), thus potentially altering an individual's overall contribution to the persistence and expansion of a colonizing population. For shifting species, pockets of favorable habitat that provide conditions which increase reproductive success within colonized suboptimal

ecosystems could play a key role in the fitness, persistence, and continued expansion of the population. Habitats that replicate conditions a species encounters in its historic habitat are particularly likely to provide an increase in reproductive fitness. These "analogous habitats", so named because they act as ecological analogues to a historically-preferred habitat, are often artificial and provide improved conditions for organisms over a surrounding suboptimal environment, thus mitigating some negative habitat effects (Lundholm & Richardson 2010 and references therein, Cannizzo et al. 2018). Such improved conditions could raise reproductive potential through a range of mechanisms that allow for an increase in the quantity and quality of reproductive investment. If analogous habitats increase the reproductive potential of range shifting species, they could play a vital role in the success of range shifts and be critical factors in the prediction of range shift outcomes.

The range expansion of the mangrove tree crab *Aratus pisonii* allows for an examination of how habitat effects of both a colonized suboptimal ecosystem and an analogous habitat therein impact the reproductive potential of a range shifting species at the range-edge. The northern range expansion of this arboreal crab has recently outpaced that of the neotropical mangroves with which its ecology and range have historically been closely tied (Rathbun 1918, Warner 1967, Riley et al. 2014). As a result, *A. pisonii* has colonized salt marshes along the South Atlantic coast of the United States, an ecosystem it had not previously inhabited (Rathbun 1918, Warner 1967, Riley et al. 2014) and which provides a suboptimal habitat. Compared to conspecifics in their historic mangrove habitat, individuals found in the marsh experience poor thermal and foraging conditions (Cannizzo et al. 2018), smaller body size (Riley & Griffen 2017, Cannizzo et al. 2018),

altered behavior (Cannizzo & Griffen 2016, Cannizzo et al. 2018), and reduced larval quality (Riley & Griffen 2017). Yet, *A. pisonii* are also found on boat docks within the salt marsh. Docks act as a habitat analogue to the mangrove by providing *A. pisonii* with improved thermal and foraging conditions compared to the surrounding salt marsh, resulting in larger individual size among other physiological and behavioral benefits (Cannizzo et al. 2018). Docks may also increase the reproductive potential of *A. pisonii* over conspecifics elsewhere in the marsh by counteracting some of the negative habitat effects they experience, thereby playing an important role in the success and expansion of this range shifting species.

We sought to determine if docks increase the reproductive potential of *A. pisonii* within the colonized salt marsh by comparing the quantity and quality of offspring produced in these two habitats to each other and to conspecifics in the historic mangrove. These primary measures of individual reproductive potential are critical to the success and expansion speed of colonizing populations (Colautti et al. 2006, Simberloff 2009) and have carry-over effects for later life stages (Grosberg & Levitan 1992, Giménez & Anger 2003). We further explored the mechanisms behind any observed differences by comparing the quantity and quality of maternal reproductive investment between the three habitats through both the proportional energetic investment into reproduction and individual measures of egg quality. These included egg energy content, which impacts larval quality (Rebolledo & Wehrtmann 2016), egg glycogen content, an important constituent of arthropod reproductive investment (Geister et al. 2008, Tropea & Greco 2015), and egg lipids, which are the most important component of embryonic development (García-Guerrero et al. 2003, Koopman & Siders 2013). In addition, we

explored the fatty acids (FA) that made up the egg lipids as they are critical to offspring quality and provide measures of the quality of both maternal reproductive investment and diet (Beltz et al. 2007, Rosa et al. 2007, Koopman & Siders 2013). Given the breadth of factors investigated, this study represents a thorough exploration of habitat-specific impacts on the reproductive fitness of a range shifting species that may be applicable to a variety of taxa while highlighting the contribution of individual mechanisms necessary for accurate modelling and prediction. Ultimately, we hypothesized that *A. pisonii* found on docks would display quantitatively and qualitatively superior reproduction compared to conspecifics in the surrounding salt marsh as a result of dietary differences between habitats.

4.3 Methods

4.3.1 Energetic Investment

To examine reproductive effort, we haphazardly collected 15 individuals by hand on each of nine randomly selected days in each habitat (Table 4.1) over two consecutive summers (n=135/habitat). Crabs were immediately placed on dry ice and kept frozen until dissection. We then calculated the gonadosomatic index (GSI) of each crab as the ratio of the dry weights of the reproductive (eggs and gonads) and somatic tissues (Kyomo 1988), which were dried separately at 60-70 ^{o}C. However, as GSI is dependent on sex and reproductive stage, we grouped crabs as male, ovigerous (egg-carrying) female, or non-ovigerous female to independently compare the proportional energetic investment into reproduction of each group between habitats. GSI represents the total reproductive investment, independent of individual size, allowing the GSI of ovigerous

females to be compared to reproductive outcomes, particularly those such as size-independent egg production and larval quality, to infer return on energetic investment. During transportation, the legs of 10 crabs collected from the mangrove became detached and mixed making it impossible to reliably obtain a weight for somatic tissue and resulting in a sample size of 125 crabs from the mangrove. Data were pooled across years for analysis as the GSI did not differ between years in any group (Tukey's HSD, $p>0.05$). We compared the GSI between habitats using an independent analysis of variance (ANOVA), followed by a Tukey's HSD test for multiple comparisons, for each sex and reproductive stage.

4.3.2 Larval Quality

We examined larval starvation resistance and larval size upon hatching - both common measures of offspring quality in crustaceans (Mashiko 1985, Giménez & Anger 2003, Sato & Suzuki 2010). For both measures, we took advantage of the lunar synchronization of *A. pisonii* reproduction (Warner 1967) by collecting five ovigerous females from each of three sites in each habitat (Table 4.1) during the week preceding the August full moon. These 45 crabs (15/habitat) were maintained at 28-30 ^{o}C in individual aquaria (22.8·15.2·16.5 cm, l·w·h) with a petri dish of 0.2 μm filtered sea water and food from their ecosystem of origin (*Spartina alterniflora* for dock and salt marsh, *Rhizophora mangle* leaves for mangrove). Food was changed every other day and water was changed daily. Crabs were checked twice daily (8am and 11pm) for release of larvae into the water dish, which always occurred after nightfall, and no crab was housed for more than eight days before larval release.

Upon larval release, crabs were euthanized and dissected at which time we determined body size measured as carapace width, and the width of the cardiac stomach to the nearest 0.1 mm. We then calculated the gut-width:carapace-width ratio for each crab: a proxy for long-term diet quality (Griffen & Mosblack 2011). In addition to the maternal dissections, 10 larvae from each brood were randomly collected, preserved in 95% ethanol, and, at a later date, dried to constant weight at 60-70 ºC. An additional 10 larvae were transferred to individual autoclaved 13·100 mm glass culture tubes containing ~6 ml of 0.2 μm filtered sea water. These larvae (n=150/habitat) were checked daily for survival, at which time a water change of ~2 ml was performed. Once all larvae died, we examined larval starvation resistance using a cox proportional hazards model with habitat, maternal size, and maternal gut-width:carapace-width ratio (GW:CW) as explanatory variables for the number of days survived. We also included maternal ID as a random factor to account for non-independence of larvae from the same mother. A linear mixed model with the same variables was used to compare larval size, as dry mass, between habitats. In both models, data were pooled between sites as no site effects were detected ($p>0.10$).

4.3.3 Crab Collection for Clutch Size and Egg Quality Analyses

We collected 20 ovigerous females by hand and from each habitat (Table 4.1) during the week preceding the full moon of each of five consecutive months throughout the *A. pisonii* reproductive season (June-October). While *A. pisonii* reproduction is often described as continuous (Warner 1967, Díaz & Conde 1989), such studies have been performed in the tropics where conditions encourage year-round reproduction (Emmerson 1994). In contrast, we found scarcely any ovigerous females in May and

November, and none from December-April. Collected crabs were immediately placed on dry ice and stored at -80 ºC until dissection at which time the size and GW:CW were determined and the whole egg mass was carefully removed. A small number of eggs (~50) were observed via microscopy to identify development stage (Rosa et al. 2007) after which they were returned to the egg mass. The eggs of the first 10 crabs from each monthly sampling in each habitat found to be carrying stage-1 non-eyed eggs were freeze-dried, stored at -80 °C, and used for lipid and glycogen analyses (see below). The eggs of the remaining 10 crabs were used to analyze clutch size and egg energy content (see below). Unless otherwise stated, all analyses had a sample size of 50 individuals per habitat.

4.3.4 Clutch Size

To determine the quantitative offspring production of *A. pisonii* in each habitat, we examined the sizes of their egg clutches. We counted the eggs (~200) in a subset of the clutch of each crab and separately dried both this subset and the rest of the clutch to a constant weight at 60-70 ºC. The total clutch size was then determined by dividing the mass of the full clutch by the average mass of an individual egg in this subset. We then stored the dried clutches individually for later analyses.

As clutch size scales with maternal size in *A. pisonii* (Leme & Negreiros-Fransozo 1998, Riley & Griffen 2017), we first compared clutch size between habitats independent of other factors using an ANOVA followed by a Tukey's HSD test. As the average size of *A. pisonii* differs between habitats (Cannizzo et al. 2018), this allowed for a comparison of the quantitative offspring production of individual crabs independent of

other factors. We then compared clutch size between habitats while controlling for differences in maternal size by obtaining the residuals of the relationship between crab size and clutch size and comparing these values between habitats using a linear model with habitat, month of collection, and GW:CW as explanatory variables.

4.3.5 Egg Energy Content

After re-drying the clutches used to determine cutch size, we used a Parr semi micro bomb calorimeter to determine the energy content of the eggs (kJ/g) and compared this value between habitats using a linear model with habitat, month of collection, maternal size, and GW:CW as explanatory variables. Unless otherwise stated, these explanatory variables were employed in all subsequent linear models. Egg stage was also added as an explanatory factor to account for variation attributable to developmental stage. Some clutches were pooled within habitats, months, and development stage to meet the minimum mass required for calorimetric analysis, resulting in sample sizes from the salt marsh of 9 in June, 8 in September, and 5 in October as well as 9 clutches from the mangrove in October.

4.3.6 Egg Lipid and Fatty Acid Content

We examined the egg lipids of each of the crabs collected from each habitat (10/month, n=50/habitat) that held stage-1 non-eyed eggs (see above). Lipids from a subset (20-40 mg) of each clutch were extracted using a modified Folch Extraction (Folch et al. 1957, Hara & Radin 1978, see Appendix B) and egg lipid content, as percent weight, was compared between habitats using a linear model. Lipids were then flushed with nitrogen and stored at -80 ^{o}C (<2 weeks).

We analyzed the diversity and quantity of the FAs found in the lipids of six randomly-selected egg masses from each habitat each month (n=30/habitat; see Appendix B for detailed methods). Briefly, we modified the methods of Morrison and Smith (1964) to methylate the FAs and analyzed the samples via gas chromatography-mass spectrometry using an Agilent Technologies 6890N Network equipped with a 30 m Restek FAMEWAX column (0.25 mm ID, 0.25μm df) connected to an Agilent 5975 Network Mass Selective Detector. The concentration of each FA (μg FA/μg egg) was then determined via dilution curves derived from a Supelco 37 Component FAME Mix (Sigma Aldrich CRM47885). While we determined the concentration of all FAs, we focused our analyses on those FAs critical to crustacean development and larval quality, including the total Omega-3 FAs (Ω-3), the individual Ω-3s eicosapentaenoic acid (EPA), docosahexaenoic acid (DHA), and alpha-linolenic acid (ALA), the Omega-3:Omega-6 ratio (Ω-3:Ω-6), and the highly unsaturated fatty acids (HUFA, $\geq$ 4 double bonds) (Yamaoka & Scheer 1970, Cahu et al. 1995, Beltz et al. 2007, Rosa et al. 2007, Rey et al. 2017). As maternal diet impacts larval quality (Helm et al. 1973), we also explored the fatty acid trophic markers (FATM) of EPA:DHA ratio, a measure of trophic position (Auel et al. 2002, Rosa et al. 2007), and the concentration of odd-numbered fatty acids (OFA), a measure of relative detritivory (Rosa et al. 2007).We compared the concentration of the FAs, FA groups, and FATMs between habitats using individual linear models.

4.3.7 Egg Glycogen Content

Following the manufacturer instructions, we used a Sigma-Aldrich Glycogen Assay Kit MAK016 to determine the glycogen concentration, as a percentage of egg

mass, of a subset (~10mg) of each stage-1 clutch. We compared these concentrations between habitats with a linear model.

4.3.8 Demographics

The body size of all ovigerous females were compared between habitats using an ANOVA followed by a Tukey's HSD test. Further, we compared the size distributions of ovigerous females in each habitat using Komlogorov-Smirnov (K-S) tests.

4.4 Results

4.4.1 Energetic Investment

Due to the large number of statistical tests performed, here we present only the resulting p-values (See Table C.1 for full statistical output associated with each result). The proportion of energy that males, ovigerous females, and non-ovigerous females invested into reproduction differed for each group between habitats (males: $p<0.001$; ovigerous females: $p<0.001$; non-ovigerous females: $p<0.001$). Both males and ovigerous females from the salt marsh invested a greater proportion of their energy into reproduction than conspecifics of the same sex/reproductive stage from the dock and mangrove habitats, which did not differ from each other (males: salt marsh vs. dock: $p<0001$, salt marsh vs. mangrove: $p<0.001$, mangrove vs. dock: $p=0.451$; ovigerous females: salt marsh vs. dock: $p=0.021$, salt marsh vs. mangrove: $p<0.001$, mangrove vs. dock: $p=0.118$; Fig. 4.1). In contrast, non-ovigerous females in the mangrove invested the lowest proportion of their energy into reproduction while conspecifics of the same reproductive stage in the dock and salt marsh habitats did not differ (mangrove vs. salt marsh: $p=0.0423$, mangrove vs. dock: $p<0.001$, dock vs. salt marsh: $p=0.0550$; Fig. 4.1).

4.4.2 Larval Quality

Larval starvation resistance was not impacted by maternal size or GW:CW ($p=0.120$ and 0.880 respectively). Thus, these variables were removed to simplify the model. Larvae originating from the mangrove displayed greater starvation resistance than those from either the dock or salt marsh ($p<0.001$, Fig 4.2a) while larvae originating from docks showed greater starvation resistance than those from the salt marsh ($p=0.009$, Fig 4.2a).

Larval size at hatching did not differ between habitats (dock vs. salt marsh: $p=0.781$, dock vs. mangrove: $p=0.604$, mangrove vs. salt marsh: $p=0.525$; Fig. 4.2b) and was not affected by maternal size ($p=0.222$). However, larval size increased with GW:CW ($p=0.025$).

4.4.3 Clutch Size

Crabs found in the salt marsh had smaller clutches than conspecifics from either the mangrove or dock habitats ($p<0.001$; Fig 5.3a), which did not differ ($p=0.994$; Fig. 4.3a). When clutch size was explored independent of maternal size, it was not impacted by GW:CW ($p=0.275$) but was affected by month of collection, with crabs producing smaller clutches in October compared to July and September and larger clutches in July compared to June and August (LM: $p<0.05$). Further, crabs from the mangrove had smaller size-independent clutch sizes than conspecifics in the dock and salt marsh habitats ($p=0.038$ and 0.034 respectively; Fig. 4.3b) whose size-independent clutch sizes did not differ ($p=0.989$; Fig. 4.3b) despite the higher proportional energetic investment (GSI) in the salt marsh.

4.4.4 Egg Energy Content

Egg energy content was not impacted by habitat (dock vs. mangrove: $p=0.971$; dock vs. salt marsh: $p=0.459$; mangrove vs. salt marsh: $p=0.522$; Fig. C.2), month of collection ($p>0.05$), or maternal variables (size: $p=0.679$; GW:CW: $p=0.728$). However, non-eyed (stage-1) eggs had a higher energy content than eyed (stages 2 and 3) eggs ($p<0.001$).

4.4.5 Egg Lipid and Fatty Acid Content

Aratus pisonii in the mangrove habitat produced eggs with a higher gross lipid content than conspecifics in either the salt marsh or dock habitats ($p<0.001$; Fig. 4.4a), which did not differ ($p=0.725$; Fig 4.4a). While egg lipid content was not impacted by either maternal size or GW:CW ($p=0.452$ and 0.834 respectively), eggs produced in October displayed higher lipid contents than those produced in June and August ($p<0.001$). Yet, the lack of an interaction between habitat and month of collection (LM: $p>0.05$) suggests that this seasonal effect was not habitat specific.

Here we present only the results of those FAs and FA groups of particular importance to reproductive potential and larval quality (See Table C.2 for full results). Unless otherwise stated, maternal size, GW:CW, and month of collection had no effect on any FA parameter ($p>0.05$). Eggs deriving from the dock habitat had the highest concentration of Ω-3s (vs. mangrove: $p<0.001$; vs. salt marsh: $p=0.010$; Fig. 4.4b) including EPA (vs. mangrove: $p=0.005$; vs. salt marsh: $p=0.005$) and DHA (vs. mangrove: $p<0.001$; vs. salt marsh: $p<0.001$). While eggs originating from the mangrove had the lowest concentration of EPA (vs. salt marsh: $p<0.001$), they did not differ from

salt marsh eggs in the concentration of overall Ω-3s or DHA ($p=0.461$ and 0.190 respectively). Further, the ALA concentration was highest in eggs originating from the mangrove (vs. dock: $p<0.001$; vs. salt marsh: $p=0.0258$) while those deriving from the dock and salt marsh did not differ ($p=0.189$). However, eggs originating from the dock had the highest HUFA concentration with those originating from the mangrove exhibiting the lowest (dock vs. mangrove: $p<0.001$; dock vs. salt marsh: $p=0.002$; mangrove vs. salt marsh: $p=0.003$; Fig. 4.4d). Despite their relatively low concentration of Ω-3s, eggs originating from the mangrove had an Ω-3:Ω-6 ratio similar to those from the dock and salt marsh habitats ($p=0.075$ and 0.564 respectively; Fig. 4.4c) while eggs originating from docks displayed a higher Ω-3:Ω-6 ratio than those from the surrounding salt marsh ($p=0.046$; Fig. 4.4c). The Ω-3:Ω-6 ratio also increased with increasing maternal size ($p=0.040$) resulting in an overall higher ratio in eggs from the mangrove compared to the salt marsh despite the insignificant effect of habitat. There were few seasonal effects, all of which were independent of habitat (LM: habitat*month: $p>0.05$), with eggs gathered in October displaying higher HUFA concentrations than those collected in June or July ($p=0.0495$ and 0.009 respectively) and higher EPA concentrations than those collected in July ($p=0.005$).

Eggs originating from the salt marsh exhibited the highest EPA:DHA ratio suggesting a lower maternal tropic position than conspecifics in the dock and mangrove habitats ($p<0.001$; Fig. 4.5a), whose eggs did not differ in this measure ($p=0.078$; Fig. 4.5a). Instead, eggs from the salt marsh displayed a higher concentration of OFAs than those from docks ($p=0.019$; Fig. 4.5b) suggesting a greater importance of detritus in the maternal diet. The OFA concertation of eggs from the mangrove did not differ from the

dock or salt marsh (p=0.157 and 0.318 respectively; Fig. 4.5b). Egg OFA concentration also decreased with increasing GW:CW (p=0.022).

4.4.6 Egg Glycogen Content

Egg glycogen content did not differ between habitats (dock vs. mangrove: p=0.107; dock vs. salt marsh: p=0.402; mangrove vs. salt marsh: p=0.743; Fig. C.3) and was not affected by GW:CW (p=0.612) or month of collection (p>0.05). However, egg glycogen content decreased with increasing maternal size (p<0.001).

4.4.7 Demographics

The smallest and average sizes of ovigerous females differed between habitats with salt marsh crabs becoming reproductively active at a smaller size than conspecifics in the dock and mangrove habitats while those from the dock were smaller than those from the mangrove (Saltmarsh: Smallest=8.0, Avg.=12.2±1.6; Docks: Smallest=11.1, Avg.=17.0±2.2 ; Mangrove: Smallest=13.4, Avg.=18.1±2.5; dock vs. mangrove: p<0.001, dock vs. salt marsh: p<0.001; mangrove vs. salt marsh: p<0.001; Fig. C.1). The size distributions of ovigerous females also differed between habitats (dock vs. mangrove: p=0.002; dock vs. salt marsh: p<0.001; mangrove vs. salt marsh: p<0.001; Fig. C.3)

4.5 Discussion

Our results demonstrate that an artificial analogous habitat within a colonized suboptimal ecosystem can increase the reproductive potential and fitness of a colonizing range shifting species. For our system, this manifests as docks providing a superior

reproductive habitat than the surrounding salt marsh. Crabs found on docks produced greater numbers of higher quality larvae for a lower per-egg energetic investment than conspecifics elsewhere in the salt marsh (Fig. 4.6). Further, the disparity in larval quality appears to be driven by differences in the quality of maternal investment reflected in the egg fatty acids (Fig. 4.6). While there is likely some travel between the dock and salt marsh habitats, this would minimize observed differences making our results conservative and strengthening their explanatory power.

Despite the benefits provided by analogous habitats, our results suggest that they may remain a subpar reproductive habitat compared to the historic ecosystem of a range-shifter (Fig 4.6). In fact, *A. pisonii* in the mangrove produced the highest quality larvae. This is unsurprising, as organisms would be expected to reproduce most successfully under conditions to which they are adapted. However, the higher size-corrected clutch-sizes (i.e. per-size offspring production) of conspecifics in the dock and salt marsh habitats may counteract some of the reproductive fitness lost to larval quality. It is common for individuals in range-edge populations to produce more offspring than conspecifics in the range-core, who tend to apply a strategy of quality over quantity (Chuang & Peterson 2016 and references therein). The higher lipid content of eggs from the mangrove further reflects these differing strategies. Yet, the dock habitat appears to allow *A. pisonii* to straddle these two strategies, producing large numbers of intermediate-quality larvae, and thus reflects a theoretical "mid-range" reproductive habitat despite occurring at the range-edge. Thus, while the historic ecosystem provides the ideal reproductive habitat, the artificial analogue is superior to the surrounding colonized ecosystem, a pattern we expect will hold true across systems.

The increased reproductive potential of crabs on docks relative to the surrounding salt marsh emphasizes the potential importance of analogous habitats, and habitat effects in general, to range shifting species while the egg quality parameters suggest the mechanism behind the acquired benefits. The only measure that differed between the dock and salt marsh was the FA profiles. As the FAs invested in eggs are crucial to larval quality (Yamaoka & Scheer 1970, Beltz et al. 2007) and reflect maternal diet (Smith et al. 2004, Rosa et al. 2007), it is likely that more favorable dietary conditions found on docks (Cannizzo et al. 2018) are largely responsible for the improved larval quality. This is further reflected by eggs from docks exhibiting higher concentrations of the developmentally critical Ω-3s, EPA, DHA (Yamaoka & Scheer 1970, Rosa et al. 2007), and HUFAs (Cahu et al. 1995, Rey et al. 2017), as well as the higher neurogenesis-stimulating Ω-3:Ω-6 ratio (Beltz et al. 2007); all of which also indicate a higher quality investment deriving from a high-quality diet (Smith et al. 2004, Beltz et al. 2007, Koopman & Siders 2013). The low EPA:DHA ratio of eggs from docks further supports this hypothesis by indicating a higher trophic position (Auel et al. 2002, Rosa et al. 2007). This suggests the dietary origin of the improved investment is animal material, a high-quality food source preferred by *A. pisonii* (Erickson et al. 2008) which is likely an important dietary component on docks (Cannizzo et al. 2018). In contrast, the high concentration of OFAs in salt marsh eggs suggests a higher dietary dependence on low-quality detritus (Rosa et al. 2007).

Diet appears to be the most important measured factor affecting offspring quality in this system and is likely to be a factor in many analogous habitats. While the mechanism of greatest importance may change from system-to-system, analogous

habitats provide a suite of conditions that can lead to increased reproductive potential and fitness for range shifting populations. Analogous habitats will often positively influence environmental parameters, which can have drastic impacts on offspring quality (Helm et al. 1973). For example, crabs in the salt marsh experience higher temperatures during the reproductive season than conspecifics in either the mangrove or dock habitats (Cannizzo et al. 2018). Higher incubation temperatures have been shown to alter the biochemical makeup (Smith et al. 2002) and development (Zeng 2007) of crustacean larvae and likely increase embryonic metabolic rates and the use of yolk reserves in the salt marsh. These effects could translate to lower starvation resistance and dispersal ability. The sum of the benefits provided by an analogous habitat could also increase reproductive potential through improved physiology and body-state. In *A. pisonii*, this effect is perhaps best represented by the increased return on reproductive investment (more eggs per unit energetic investment) found in crabs on docks. The fact that crabs grow larger on docks, likely due to a combination of improved thermal and dietary conditions (Cannizzo et al. 2018), further increases the quantity of offspring they produce. The importance of this effect to the reproductive potential of the population is not yet known, but results here suggest that individuals on docks make an important reproductive contribution to the expanding range of this species. Given the importance of reproduction to colonization success (Colautti et al. 2006, Simberloff 2009) and the relatively small area of analogous habitats within colonized ecosystems, individuals occupying analogous habitats could play vital roles in the persistence and continued expansion of shifting species. Habitat analogues may even accelerate the rate of expansion through the production of more

and/or higher quality offspring. As such, understanding the role of analogous habitats will be critical for the management and prediction of range-shifts.

Many habitat analogues are artificial (Lundholm & Richardson 2010 and references therein), providing a unique opportunity for the conservation and management of range shifting species. Through the installation, alteration, or removal of analogous habitats, managers may be able to manipulate habitat effects and target reproductive hot-spots of range-shifters thus encouraging or reducing their spread and persistence. For instance, artificial structures could provide habitats to shifting mangrove-associated species, a habitat which is globally threatened (Sandilyan & Kathiresan 2012), and even be used as a mitigation and dispersal corridors in areas of mangrove deforestation. The establishment of corridors between favorable habitats is a commonly discussed strategy to aid range shifting species (Hannah 2001, Krosby et al. 2010) and artificially modified habitats have been used to improve conditions in climate-impacted native ecosystems (Mitchell et al. 2008, Shoo et al. 2011). However, habitat construction has not been a focus in managing the climate-mediated range-shifts of native species into new ecosystems (but see Hoegh-Guldberg et al. 2008). In such instances, species are not simply moving between fragments of historically-favored habitat, but colonizing entirely new ecosystems where novel habitat effects will likely play a permanent role in the persistence of the population. Our results suggest that the strategic placement or modification of artificial structures within these natural, but suboptimal, ecosystems could increase the reproductive success of range shifting species that are reproduction-limited and, given the relatively small size of these habitats, play an outsized role in their persistence and rate of shift in a colonized ecosystem.

While habitat effects are likely of greatest importance to larval and seed dispersers, even mobile adult-dispersing species could receive reproductive benefits from habitat analogues through mechanisms such as predation refuge or improved diet and body condition. This potential of artificial habitat analogues to mitigate negative habitat effects and increase the reproductive fitness of shifting species has broad applicability across systems. Despite the relative lack of study on the role of analogous habitats during range shifts (but see Grant 2006, Grieg et al. 2017), they could provide a vital reproductive boost for shifting populations encountering suboptimal conditions. If the benefits documented here are general across systems, the role of artificial habitat analogues in altering reproductive fitness could be important to the management and success of future range shifting species. Thus, both habitat analogues and habitat effects represent understudied phenomena in range-shift ecology that merit further investigation in the study and management of range-shifts.

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4.7 Tables

Table 4.1. Locations of collection sites. X's denote which sites were used in each aspect of the study.

Habitat	Site	Lat-Long	Energetic Investment	Egg Quality	Larval Quality
Mangrove	Pepper Park	27°29'42"N 80°18'12"W	X	X	X
Mangrove	Round Island Park	27°33'33"N 80°19'53"W	X	X	X
Mangrove	Oslo Road	27°35'14"N 80°21'55"W	X	X	X
Mangrove	North Causeway	27°28'28"N 80°19'12"W	X	X	
Mangrove	Bear Point	27°25'48"N 80°17'10"W	X		
Salt Marsh	GTM NERR	30°0'49"N 81°20'42"W	X	X	X
Salt Marsh	Anastasia State Park	29°52'40"N 81°16'32"W	X	X	X
Salt Marsh	Vilano Marsh	29°55'16'N 81°17'57"W		X	X
Dock	Palm Valley	30°07'57"N 81°23'08"W	X	X	X
Dock	Yacht Club	29°53'09"N 81°17'08"W	X	X	X
Dock	Boating Club	29°56'34"N 81°18'31"W		X	
Dock	Vilano Dock	29°56'33"N 81°18'32"W			X

4.8 Figures

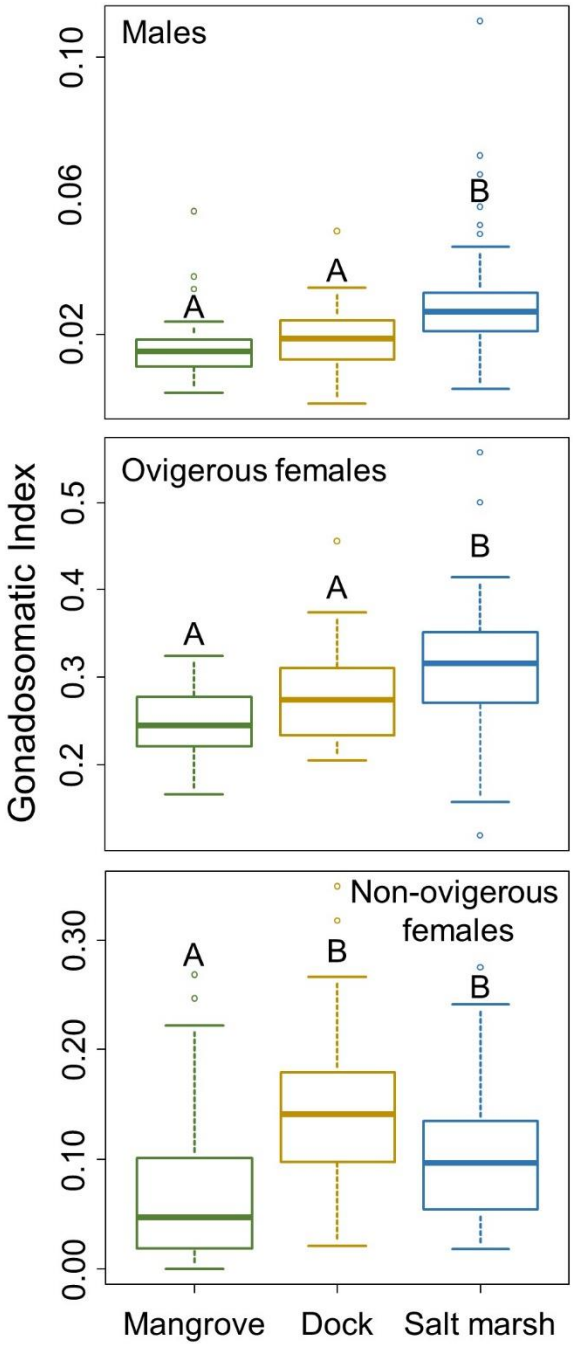


Figure 4.1. Proportional energetic investment into reproduction, calculated as gonadosomatic index, of male, ovigerous female, and non-ovigerous female *A. pisonii* in different habitats. Letters denote homogeneous groups in this and all other figures presented in this paper. In each boxplot, and in all other boxplots presented in this paper, the median is represented by a heavy line, the box represents the upper and lower quartiles, while the whiskers represent 95% of the data and circles show outliers.

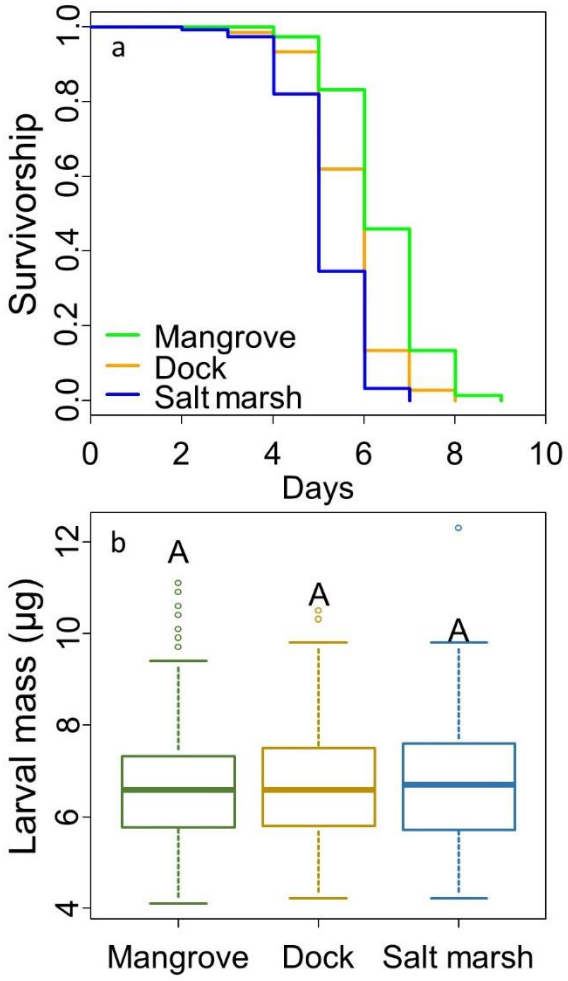


Figure 4.2. (A) Kaplan-Meier curves comparing starvation resistance of *A. pisonii* larvae from different habitats. (B) Comparison of larval size at hatching, measured as larval dry mass, between habitats.

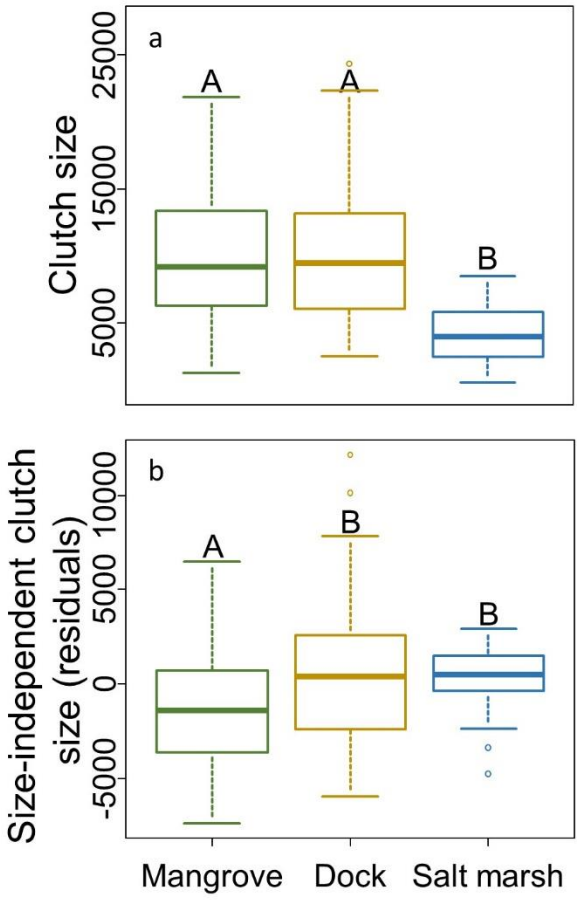


Figure 4.3. (A) *Aratus pisonii* clutch-size in different habitats. (B) Size-independent clutch size in different habitats represented by residuals of the relationship between crab size and clutch size.

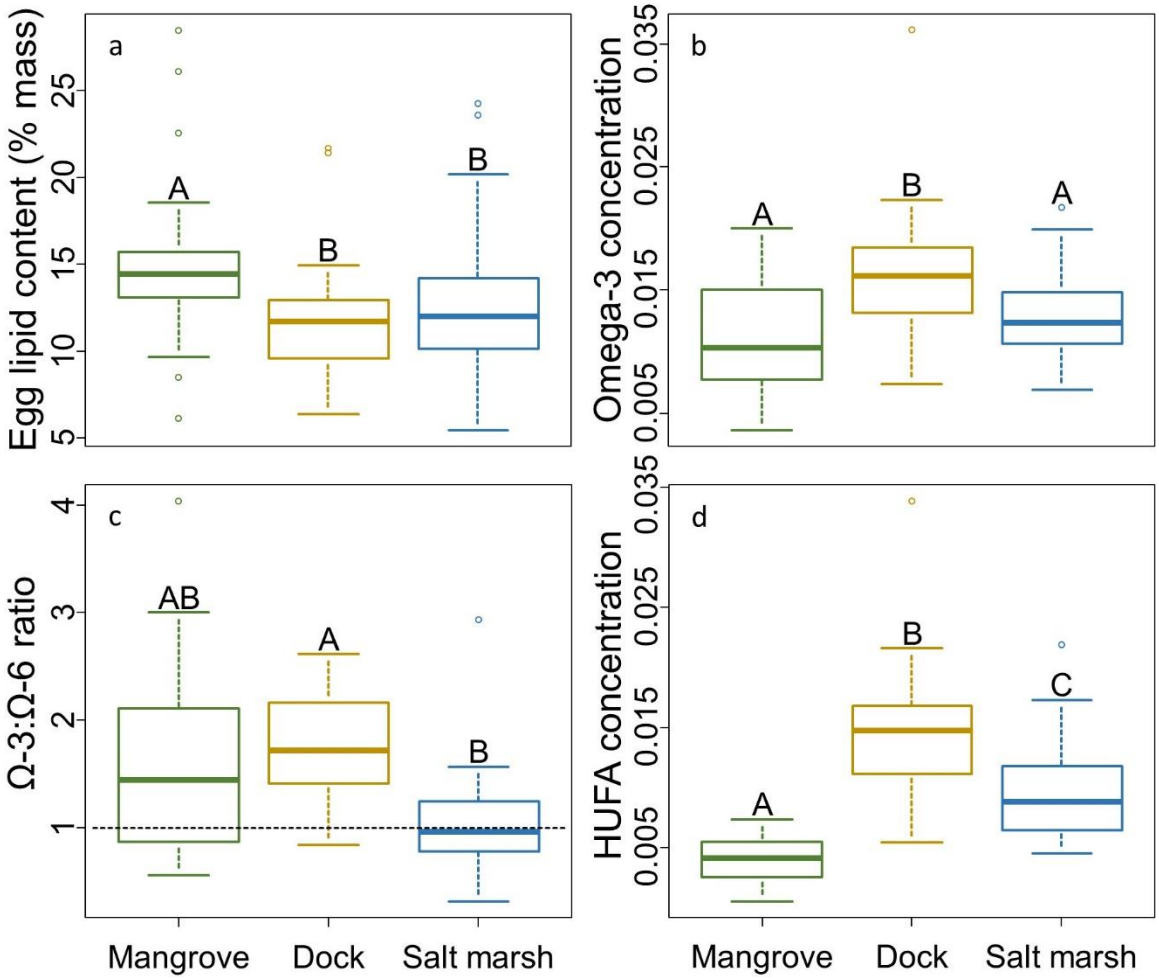


Figure 4.4. (A) Gross lipid content of *A. pisonii* eggs originating from each habitat as percent of egg mass. (B) Ω-3 fatty acid content of eggs originating from each habitat as proportion of egg mass. (C) Ω-3:Ω-6 ratio of eggs originating from each habitat. Horizontal line represents a 1:1 ratio. (D) Concentration of HUFA in eggs originating from each habitat.

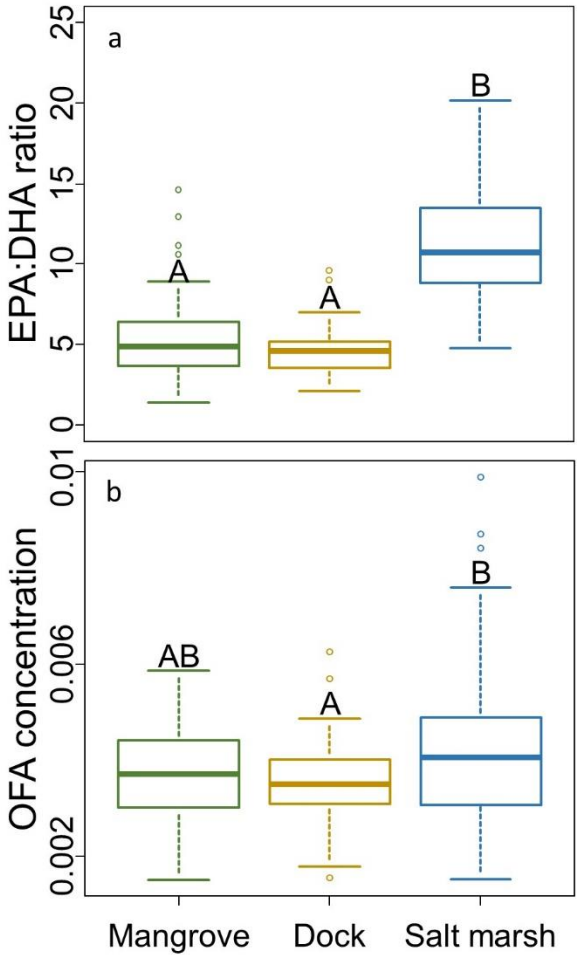
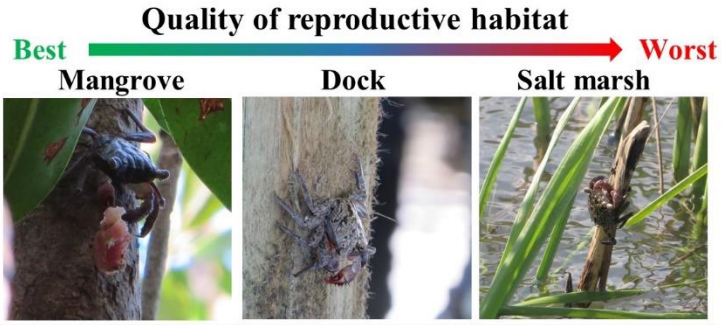


Figure 4.5. (A) EPA:DHA ratio of eggs originating from each habitat. (B) Concentration of odd-numbered fatty acids of eggs originating from each habitat.



	Mangrove vs. Dock	Dock vs. Salt marsh	Salt marsh vs. Mangrove	Origin of Conclusions
Total Egg Production	=	↑	↓	Clutch Size
Eggs Produced per Energetic Investment	↓	↑	–	GSI + Size-independent Clutch Size
Larval Quality	↑	↑	↓	Larval Starvation Resistance + Larval Size
Egg Gross Lipid Content	↑	=	↓	Egg Lipid Concentration
Egg Fatty Acid Quality	–	↑	–	Ω-3 + EPA + DHA + ALA + HUFA + Ω-3:Ω-6
Diet	=	↑	↓	EPA:DHA + OFA

Figure 4.6. Summary of the conclusions drawn from the results of this study. Green arrow indicates the first habitat in the comparison is better for the result being compared while a red arrow indicates it is worse and a blue equal sign indicates the habitats did not differ. A black dash indicates an inability to draw a conclusion between the compared habitats.

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CHAPTER 5

HABITAT SPECIFIC IMPACTS OF HURRICANE MATTHEW ON A RANGE EXPANDING SPECIES[1]

[1] Cannizzo ZJ & Griffen BD. 2018. Habitat specific impacts of Hurricane Matthew on a range expanding species. *Hydrobiologia*. 809: 79-89.
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5.1 Abstract

As range shifting species colonize new ecosystems they may experience novel conditions that may alter their ability to mitigate impacts of periodic disturbances. Here we explore how the impact of Hurricane Matthew on the mangrove tree crab (*Aratus pisonii*) differed between its historic and colonized habitats. As this species responds to flood waters by climbing structure, we predicted that structural differences between habitats would generate habitat dependent impacts. Through field surveys, we found that crabs in the historic mangrove habitat, where tall structure remained unsubmerged, showed no reduction in body size as a result of the hurricane. In contrast, crabs in the colonized saltmarsh ecosystem, where all structure was submerged, exhibited a reduction in body size suggesting large crabs were disproportionately impacted. Further, crabs found on docks within the saltmarsh exhibited a body size reduction in only one of three sites. Docks are more structurally similar to mangroves and may have provided more micro-habitat refuges for large crabs than marsh grasses. Thus, structural differences between habitats appear to have altered the hurricane impact experienced by this species. The ability to mitigate disturbance impacts under novel conditions could contribute to the success of range shifting species as they colonize new ecosystems.

5.2 Introduction

Periodic disturbances impact species in all ecosystems. From fires to floods, species often evolve adaptations to survive, take advantage of, or mitigate the impacts of natural disturbances (Schwilk & Ackerly 2001, Lytle et al. 2008, Lawes et al. 2011, Gunzburger et al. 2010). If a species has evolved with a particular disturbance, that

disturbance may give it an advantage over invaders (Witt & Nogogo 2011) or, conversely, may help it colonize new ecosystems (Seabloom et al. 2003, D'Antonio & Viousek 1992). Thus, as humans and climate change continue to encourage species to colonize ecosystems they have not previously inhabited (Schweiger et al. 2008, Walther 2010), the success of these colonizing species will be impacted by natural disturbances. However, even if a species has evolved a response to a disturbance, novel conditions experienced in a colonized ecosystem may alter the effectiveness of that response leading to an alteration of the impacts experienced from the disturbance under novel conditions.

Of particular interest are periodic ecosystem-scale disturbances that occur on the time scale of years to decades such as tornadoes, fires, and hurricanes. Such disturbances are common enough that species are likely to evolve behavioral and life history strategies to mitigate their impacts. Common strategies include evacuation (Jury et al. 1995, Streby et al. 2015, Bailey & Secor 2016), sheltering (Garvey et al. 2010), and resistance (Gunzburger et al. 2010, Simon et al. 2009), and are more likely to evolve if disturbances are severe and/or frequent (Lytle 2001). Yet, these disturbances are also rare enough that a population may spend years or decades in a colonized ecosystem without experiencing one. Additionally, the impacts of these disturbances on biological communities often differ between habitats (Pearsons et al. 1991, Roy et al. 2003, Queriós et al. 2006). Thus, such periodic disturbances may have catastrophic impacts on range shifting species in colonized ecosystems if pre-evolved strategies for responding to them are inadequate under the novel conditions. Consequently, these disturbances could greatly impact the ability of a range shifting species to persist and continue to expand into a new ecosystem. Therefore, as species continue to colonize new ecosystems, exploring the relative impacts

of periodic disturbances in both historic and colonized ecosystems may help us understand and predict the long-term success of range expanding colonizers. Further, range shifts that result in the colonization of new ecosystems allow for the examination of the impact of disturbances on individual species across multiple habitats, which is understudied and often lost among examinations of community level responses (but see Olson & Platt 1995).

The mangrove tree crab (*Aratus pisonii*; H. Milne-Edwards 1837) represents an ideal system to study the impacts of disturbances on a range shifting species across multiple habitats. The climate-mediated northward range expansion of *A. pisonii* has recently outpaced that of its historic mangrove habitat (Riley et al. 2014, Saintilan et al. 2014) resulting in this Neotropical mangrove associated species colonizing the saltmarshes of the Atlantic coasts of Florida and Georgia (Riley et al. 2014). The historically arboreal *A. pisonii* has no evolutionary experience in the saltmarsh ecosystem which has proven to be a suboptimal habitat for this species resulting in altered behavior, ecology, and life history (Cannizzo & Griffen 2016, Riley & Griffen 2017). In the mangrove, this crab's ecology and behavior are closely tied to mangrove trees and the structure that they provide (Wilson 1989, Beever et al. 1979, López & Conde 2013, Cannizzo & Griffen 2016). However, these trees are absent in the saltmarsh which is instead dominated by the grass *Spartina alterniflora* (Loisel), which provides a vastly different structural habitat. Structure plays a critical role in the disturbance responses of a variety of animals (Robinson et al. 2013 and references therein) ranging from beach mice (Pries et al. 2009) and wallabies (Garvey et al. 2010) to terrestrial invertebrates (Brennan et al. 2011). Thus, the structural differences between mangrove and saltmarshes may alter

the effectiveness of the disturbance response by *A. pisonii*. In particular, the shorter, less complex structure of saltmarsh grasses could reduce the effectiveness of the climbing behavior utilized by *A. pisonii* to avoid rising waters, a behavior exhibited in all habitats where it is found (pers. obs., Warner 1967, Wilson 1989). This could lead to magnified impacts on individuals in the saltmarsh when encountered with disturbance associated flooding.

However, *A. pisonii* are also found on docks within the saltmarsh which provide habitat that is more structurally similar to the mangrove than surrounding marsh grasses. The structural similarity of docks and mangroves may allow *A. pisonii* found in these habitats to exhibit similar responses to mitigate disturbance impacts. If this is the case, docks could act as refuges during a disturbance. Refugia are often vital to the survival of individuals (Woodin 1978, Robinson et al. 2013 and references therein) and population recovery after a disturbance (Lake 2000 and references therein). Thus, if docks act as a refuge they could play a vital role in the ability of *A. pisonii* to survive a disturbance under the novel conditions experienced in the saltmarsh. With the occurrence of Hurricane Matthew, we were able to test this hypothesis and use this system to explore the influence of habitat type on the impact of a periodic natural disturbance on a range shifting species.

On September 29th, 2016, tropical storm Matthew developed into a Hurricane 310 km northeast of Curaçao. Over the next ten days it would impact the Caribbean and US East coast strengthening to a category 5 storm which produced winds topping 270 km/h and record water levels in many locales (Stewart 2017). The storm passed near Florida as a category 4 storm resulting in coastal winds topping 170 km/h and water levels over 2m

above ground level before moving northward along the Atlantic coast and out to sea (Fig 5.1; Stewart 2017).

Of the many forms of periodic disturbance, coastal species such as *A. pisonii* are particularly susceptible to hurricanes (Michener et al. 1997). In addition to direct impacts through storm surge (Schriever et al. 2009), wind (Smith et al. 1994), and post-storm flooding (Roman et al. 1994, Paerl et al. 2001, Burkholder et al. 2004), hurricanes can destroy habitat (Smith et al. 1994) and food sources (Lynch 1991, Bildstein 1993, Michener et al. 1997). Many coastal species have adapted strategies to weather these storms and minimize their impacts, such as seeking shelter (Pries at al. 2009) and evolving salinity resistance (Gunzburger et al. 2010).

One way a hurricane may impact a population is by altering its demographics. Disturbances can have age-, size-, or development-specific impacts (Willig & Camilo 1991, Smith et al. 1994, Barlow et al. 2002, Schierver et al. 2009) that can have cascading consequences for a population that persist for generations (Woolbright 1991, 1996). While we did not have pre-hurricane data on the age distribution of *A. pisonii*, we did have crab size measurements. Thus, we decided to examine if the hurricane had altered this important demographic variable. We examined whether Hurricane Matthew impacted the size distribution of crabs differently between the mangrove, saltmarsh, and docks habitats. As the mangrove and dock habitats provide taller structure that may have remained unsubmerged and provided more micro-habitat shelters, we hypothesized that crabs in the saltmarsh would experience a greater impact than conspecifics in the mangrove or on docks. We also expected that within habitats, crabs found at sites closer

to oceanic inlets would experience greater impacts due to stronger currents and flood-waters.

5.3 Methods

5.3.1 Site Description

We examined *A. pisonii* at all sites that were accessible after the hurricane and for which we had pre-hurricane size data from 2016. This resulted in data from four mangrove sites, two saltmarsh sites, and three dock sites (Table 5.1, Fig 5.1). All sites were located in estuaries and varied in distance from the nearest oceanic inlet (Fig 5.1), which we determined using Google Earth by drawing straight lines through water-ways to the nearest inlet. Mangrove sites represent areas within the historic range of *A. pisonii* (Rathbun 1918, Warner 1967) while saltmarsh and dock sites are within the newly expanded range (Riley et al. 2014) in and around St. Augustine Florida. Our mangrove sites have a primarily muddy substrate and are dominated by the red mangrove *Rhizophora mangle* (L.) with the black mangrove *Avicennia germinans* (L.) and white mangrove *Laguncularia racemosa* (L.) also present to a lesser degree. The salinity at the mangrove sites is highly variable both daily and seasonally ranging from about 17-37ppt with higher salinities in the winter and lower, more variable salinities in the summer (S. Reed unpub. data). While saltmarsh and dock sites also have a primarily muddy substrate, the ecosystem is dominated by the saltmarsh grass *S. alterniflora*. Similar to the mangrove, these sites experience salinities that vary both daily and seasonally ranging from about 10-38ppt (NERRS database, station GTMPIWQ).

While the first report of *A. pisonii* in the vicinity of St. Augustine was published in 2014 (Riley et al. 2014), local fisherman report sightings of the species in the area as early as 2005 (pers. comm). As the last hurricane to impact this area was Hurricane David in 1979, Hurricane Matthew likely represents the first hurricane-level disturbance experienced by *A. pisonii* at these saltmarsh sites. Further, Hurricane Matthew weakened as it approached the saltmarsh and dock sites (Fig 5.1). If storm strength was the only factor determining the impact experienced by *A. pisonii*, we would expect to see lower impacts in the saltmarsh ecosystem. Thus, this study represents a conservative test of our hypothesis that crabs in the saltmarsh will experience greater impacts than those in the mangrove ecosystem, since such a result would run counter to a direct association between impacts and storm strength.

5.3.2 Crab Size

Following the collection procedure of the ongoing study from which the pre-hurricane data were obtained, we collected the first 30 *A. pisonii* we encountered by hand from each site within 20 days of the passing of Hurricane Matthew (Table 5.1). While this collection occurred on a single day at most sites, ongoing studies resulted in this collection taking place over multiple days at the mangrove site Round Island (RI) and the saltmarsh site GTM NERR (Table 5.1). Further, at one mangrove site, Pepper Park (PP), we subsequently collected an additional 15 crabs on November 6th because the initial post-hurricane collection yielded only females. Another exception was the dock site Boating Club (BC) where we were only able to find 15 crabs post-hurricane. We determined the sex and carapace-width (to the nearest 0.1mm) of all crabs and released those that were not needed for ongoing studies. For pre-hurricane size data, we used the

previously recorded carapace widths of all crabs collected at each site during the ongoing field season (May-October, 2016). As this was an opportunistic study, the sample sizes and dates of collection pre-hurricane varied (Table 5.1). To prevent biasing the results due to possible recruitment between the pre and post-hurricane datasets, we eliminated any crabs smaller than the smallest known gravid female (8.0mm, unpub. data). This correction resulted in 27 individuals from the Anastasia saltmarsh site for the post-hurricane dataset and the removal of two individuals from the pre-hurricane data set at this same site (Table 5.1).

To compare the impact of Hurricane Matthew on the size of *A. pisonii* between habitats, we ran a general linear model (GLM) with habitat type and hurricane (pre or post) as explanatory factors for the dependent variable of crab size. Additionally, we used a Kologrov-Smirnov test (K-S test) for each habitat type to compare the impact of the hurricane on the distribution of crab sizes.

We then explored the impact of the hurricane on crab size separately within each habitat type. First, to determine if the hurricane had site-specific impacts within habitats, we ran a linear model (LM) for each habitat type with hurricane (pre and post) and site as explanatory factors for crab size. Each model was followed by a Tukey's HSD test to determine homogeneous groups. Finally, to explore the effect of the distance from the nearest inlet on crab size within habitats, we ran a general linear model for each habitat with hurricane and distance from the nearest inlet as explanatory factors.

Aratus pisonii is sexually dimorphic with males reaching a larger size (Warner 1967). Thus, the sex ratio of collected crabs has the potential to impact the results and

their interpretation. However, due to the fact that much of the pre-hurricane data was drawn from ongoing studies which focused on gathering females, no results can be reliably drawn from the sex-ratios of crabs pre- and post-hurricane. Therefore, we treat the sex ratios pre- and post-hurricane as a characteristic of the dataset and thus present them here to facilitate understanding of the results. The sex ratio (M/F) of *A. pisonii* in the pre-hurricane dataset was 0.286, 0.222, and 0.374 in the mangrove, dock, and saltmarsh habitats respectively. In the post-hurricane dataset, the sex ratio of *A. pisonii* was 0.581, 0.971, 0.357 in the mangrove, saltmarsh, and dock habitats respectively. We reiterate that these sex ratios, especially pre-hurricane, reflect our efforts to capture females for other ongoing studies and do not reflect the true sex ratios in the populations. However, the increase in the proportion of males in the post-hurricane dataset, especially in the saltmarsh, together with the differential size of males and females, suggests that any reduction in size seen after the hurricane is likely a conservative estimate.

In addition to sex-ratio, some crab species display temporal differentiation in size (Aagaard et al. 1995, Koga et al. 2010). In order to ensure that the inclusion of pre-hurricane data from a range of dates did not impact the results, we ran a general linear model to determine the impacts of collection day (as day of year), site, and sex on the size of *A. pisonii* pre-hurricane in each habitat. Sex and site were included in the model to account for the potentially confounding effects of pre-hurricane sampling that was both sex-biased and uneven across sites (Table 5.1). To further assure that inclusion of the full dataset did not bias the results we ran the analyses with subsets of the pre-hurricane data. These subsets included only data from July-September with the exception of the site Palm Valley which required the inclusion of data collected June 22nd and later due to the

small size of the dataset in July and September. These analyses produced qualitatively identical results to the analyses of the full dataset so we included all data for completeness.

5.4 Results

Hurricane Matthew had an overall negative impact on crab size (GLM: estim. =-0.7348, $p<0.001$; Fig 5.2a). However, this impact differed between habitats. There was a reduction in the size of the *A. pisonii* found in the saltmarsh (GLM: estim. = -1.0072, $p<0.001$; Fig 5.2a) and dock habitats (GLM: estim. = -1.0377, $p<0.001$; Fig 5.2a) but not in the mangrove (GLM: estim. = -0.3033, p= 0.2278; Fig 5.2a). In addition, the magnitude of the size reduction did not differ between the saltmarsh and dock habitats (GLM, hurricane*habitat: estim. = -0.03710, p = 0.899). Further, there was a change in the size distribution of crabs found in the saltmarsh (K-S Test: $p<0.001$; Fig 5.2d) and dock habitats (K-S Test: $p<0.001$; Fig 5.2b) with both exhibiting wider distributions shifted towards smaller sizes. In contrast, there was no change in the size distribution of crabs found in the mangrove (K-S Test: p=0.1562; Fig 5.2c). Further, all habitats displayed greater variability in crab size post-Hurricane (Fig 5.2a). However, this was not true across all sites within habitats (Fig 5.3) and may in part be an artifact of smaller sample-sizes post-hurricane.

In the mangrove, the size of crabs differed between sites (LM: F=101.8, p=0.0075; Fig 5.3). However, there was no effect of hurricane (LM: F=13.3, p=0.2076; Fig 5.3) or the interaction between hurricane and site on the size of crabs (LM: F=59.9, p=0.069; Fig 5.3). Further, no individual mangrove site saw a reduction in *A. pisonii* size

after the hurricane (LM: $p>0.05$; Fig 5.3). Finally, there was no effect of the interaction between hurricane and the distance from the nearest inlet on the size of crabs in the mangrove (GLM: estim. = -0.03592, $p=0.4669$; Fig 5.3).

In the saltmarsh, there was an effect of both site (LM: $F=119.1$, $p<0.001$; Fig 5.3) and hurricane (LM: $F=80.8$, $p<0.001$; Fig 5.3) on crab size. Further, while both sites saw a reduction in crab size after the hurricane (LM: $p<0.05$), the magnitude of this reduction differed between sites (LM, hurricane*site: $F= 23.8$, $p=0.001$; Fig 5.3). Specifically, the further a saltmarsh site was from the nearest inlet, the less the reduction in the size of the crabs found there (GLM, hurricane*distance from inlet: estim. = 0.11060, $p=0.001$).

For crabs found on docks within the saltmarsh, size differed between sites (LM: $F=252$, $p<0.001$; Fig 5.3) and was negatively impacted by the hurricane (LM: $F=171.9$, $p<0.001$; Fig 5.3). Despite the lack of a significant interaction between site and hurricane (LM: $F= 26.8$, $p=0.079$; Fig 5.3), only one dock site (Boating Club) showed a reduction in crab size (LM: $p=0.0016$; Fig 5.3). Additionally, the distance of a dock site from the nearest inlet did not affect crab size (GLM hurricane*distance from inlet: estim. = 0.01183, $p=0.6605$).

Day of the year did not have an impact on the size of crabs in any habitat (Mangrove GLM: estim. = -0.00147, $p=0.7696$; Saltmarsh GLM: estim. = -0.00202, $p=0.6245$; Dock GLM: estim. = 0.01960, $p=0.084$) suggesting that inclusion of data from a range of dates pre-hurricane was unlikely to bias the results.

5.5 Discussion

Our results suggest that *A. pisonii* was more susceptible to the impacts of Hurricane Matthew in the colonized saltmarsh ecosystem than in the historic mangrove and that this impact was disproportionately felt by large individuals. Neither the mean size nor size frequency distribution of crabs found in the historic mangrove ecosystem changed, suggesting that any hurricane induced mortality was not related to crab size. However, there was both a reduction in the mean size and a shift towards smaller sizes in the frequency distributions of crabs collected in the colonized saltmarsh ecosystem, both in the saltmarsh proper and on docks. This may reflect both the effects of the hurricane (loss of large individuals) and the growth of previously sub-adult individuals (more individuals in the small end of the size range). In addition, the abundance of *A. pisonii* both in the saltmarsh and on docks appeared much lower after the storm based on the unusually long period of time that it required to catch 30 individuals post-hurricane when compared to the ease of catching individuals pre-hurricane. In fact, at the dock site Boating Club, only 15 crabs could be found. However, as we did not have pre-hurricane abundance data this is a purely anecdotal conclusion drawn from extensive time working at these sites.

We suggest that the habitat-specific susceptibility of *A. pisonii* to the hurricane was a result of structural differences between the three habitats. In all habitats, *A. pisonii* climbs structure as the tide rises to avoid aquatic predators (pers. obs., Warner 1967, Wilson 1989). It is likely that this response was triggered by rising waters during and after the storm. In the mangrove, the canopy remained unsubmerged providing crabs with a refuge. In contrast, the storm surge and subsequent flood waters overtopped all

structure in both the saltmarsh and dock habitats for an extended time (pers. comm. local residents). During this submergence, crabs likely experienced strong currents associated with storm surge and flooding. Large crabs have a greater surface area on which such currents can act, thus increasing the drag force upon them, and are also less likely to be able to find shelter in microhabitat "nooks and crannies". This is especially true in the saltmarsh where there are few microhabitat shelters on grasses big enough for a large individual to take refuge. Current strength may also help to explain the nearly 3-fold greater drop in average size seen in the saltmarsh site closer to the inlet, where the water speed was likely higher. In addition, the inability to easily access shelter in the saltmarsh habitat may have led to a fleeing response where crabs moved inland away from the saltmarsh habitat as the storm surge rose. There is some evidence that *A. pisonii* exhibited this behavior in the saltmarsh (pers. comm. with residents). As the typical response of *A. pisonii* to rising waters is to climb structure (pers. obs., Warner 1967, Wilson 1989), this behavior is unlikely to have been exhibited in the mangrove where structure remained unsubmerged. Thus, this fleeing response, and any associated negative impacts such as stranding in unfavorable habitat, are likely to be another result of structural differences between habitats.

In contrast to marsh grasses, docks remained unsubmerged for a longer time and likely provided more micro-habitat refuges for large crabs. Further, the reduction in the size of crabs found on docks appears to be driven by one site, Boating Club, which was both the only dock site to show a reduction in crab size and the site which sustained the greatest physical damage. This suggests that the size-dependent impact exhibited by crabs on docks may have been driven largely by habitat destruction at Boating Club,

resulting in a drastic reduction in microhabitat refuges for large resident crabs. The lack of a size reduction at the other dock sites further supports this conclusion and suggests docks at those sites provided refuge for *A. pisonii*. The ability of such refuge habitats to provide increased protection during disturbances has been shown to be important to a range of taxa (Woodin 1978, Lake 2000, Robinson et al. 2013 and references therein). The importance of these disturbance refugia is likely to be magnified under novel conditions that otherwise exacerbate disturbance impacts. Thus, the presence of natural and anthropogenic habitats that provide disturbance refugia could influence range shifting species by mitigating the impacts of periodic disturbances experienced under novel conditions in colonized ecosystems.

In addition to the impact of physical factors such as habitat structure, wind stress, and rising water, it is likely that *A. pisonii* experienced changes in water chemistry that are often associated with a hurricane. In particular, hurricane associated changed in salinity can have adverse effects on numerous species (Gardner et al. 1991, Michener et al. 1997 and references therein). In the estuarine sites where *A. pisonii* is found, salinity likely rose to high levels during the storm as the storm surge moved into the estuary (Gardner et al. 1991, Michener et al. 1997), and then fell to abnormally low levels during the subsequent flooding (Van Dolah & Anderson 1991, Paerl et al. 2001). While changes in salinity may have impacted crabs during the storm if they were unable to remain out of the water, this crab is largely terrestrial and thus would unlikely be greatly impacted by changes in salinity after the storm. Further, the crabs found at the study sites are regularly exposed to relatively large daily and seasonal salinity fluctuations. Thus, while changes

in salinity may have had some impact on *A. pisonii*, it is unlikely to account for the differences in hurricane impact observed between habitats.

Ultimately, residing in either the saltmarsh proper or on docks increased the susceptibility of *A. pisonii* to Hurricane Matthew. This may be a result of complete submergence of structure in the colonized ecosystem rendering the climbing response of *A. pisonii* less effective. Alternatively, the lower structural complexity of the colonized habitats may have provided less shelter from hurricane-force winds, storm surge, and currents. Regardless of the precise cause, structural differences between the historic and colonized ecosystems appear to have resulted in increased susceptibility of individuals found in the colonized saltmarsh ecosystem. This is particularly clear given that the weakening of the storm on its northward trajectory should have resulted in lower impacts in the marsh and dock habitats, relative to the mangrove, if the refuge value of all 3 habitats had been equivalent. As hurricane intensity is expected to increase with continued climate change (Emanuel 1987, 2005), this increased susceptibility could impede this species' continued expansion into the saltmarsh. Additionally, as egg production scales with body size in *A. pisonii* (Leme & Negreiros 1998, López-Sánchez & Quintero-Torres 2015, Riley & Griffen 2017), the disproportionate impact of the hurricane on large crabs in the saltmarsh may result in a reduction in offspring production. Such a drop in reproduction as a result of a disturbance-induced decrease in adult size has previously been seen in forest frogs following Hurricane Hugo (Woolbright 1991). A similar drop in reproductive output could have consequences for the rate of the expansion and establishment of *A. pisonii* in the saltmarsh.

This study suggests that the impact of a disturbance on a range shifting species is directly affected by the habitat in which it is found because disturbance impacts may be enhanced in newly colonized habitats if the effectiveness of pre-evolved disturbance responses are compromised by habitat-specific characteristics. Even if a species can colonize a new ecosystem under normal, stable conditions, if it experiences a greater periodic disturbance impact due to novel conditions, its long-term persistence in the colonized ecosystem could be slowed or prevented.

5.6 Acknowledgments

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5.7 Tables

Table 5.1. Study sites, their distance from the nearest inlet, dates sites were visited, and the number of crabs examined.

Site	Habitat	Lat-Long	Distance From Nearest Inlet (km)	Dates Examined Pre Hurricane (# crabs examined)	Dates Examined Post Hurricane (# crabs examined)
North Causeway Park	Mangrove	27°28'28"N 80°19'12"W	4.0	8/13 (20)	10/26 (30)
Pepper Park	Mangrove	27°29'42'N 80°18'12"W	5.0	6/16 (20); 7/6 (15); 9/4 (15)	10/11 (30); 11/6 (15)
Round Island Park	Mangrove	27°33'33"N 80°19'53"W	12.7	5/25 (2); 6/2 (3); 7/15 (20); 9/30 (14)	10/21 (9); 10/26 (22)
Oslo Park	Mangrove	27°35'14"N 80°21'55"W	16.0	5/17 (15); 9/14 (20); 9/15 (18)	10/26 (30)
Anastasia State Park	Saltmarsh	29°52'40"N 81°16'32"W	4.3	7/11 (20); 7/12 (20); 9/9 (33);	10/24 (27)
GTM NERR	Saltmarsh	30°0'49"N 81°20'42"W	13.5	6/14 (19); 6/26 (12); 7/9 (14); 7/25 (15); 8/15 (21)	10/13 (21); 10/19 (21)
Yacht Club	Docks	29°53'09"N 81°17'08"W	3.8	7/10 (15); 7/12 (34); 7/23 (15)	10/12 (30)
Boating Club	Docks	29°56'34"N 81°18'31"W	4.6	8/16 (20)	10/20 (15)
Palm Valley	Docks	30°07'57"N 81°23'08"W	20.4	6/8 (5); 6/22 (23); 6/23 (24); 6/24 (23); 6/25 (22); 7/24 (3); 8/16 (3); 9/11 (2)	10/18 (5); 10/23 (26)

5.8 Figures

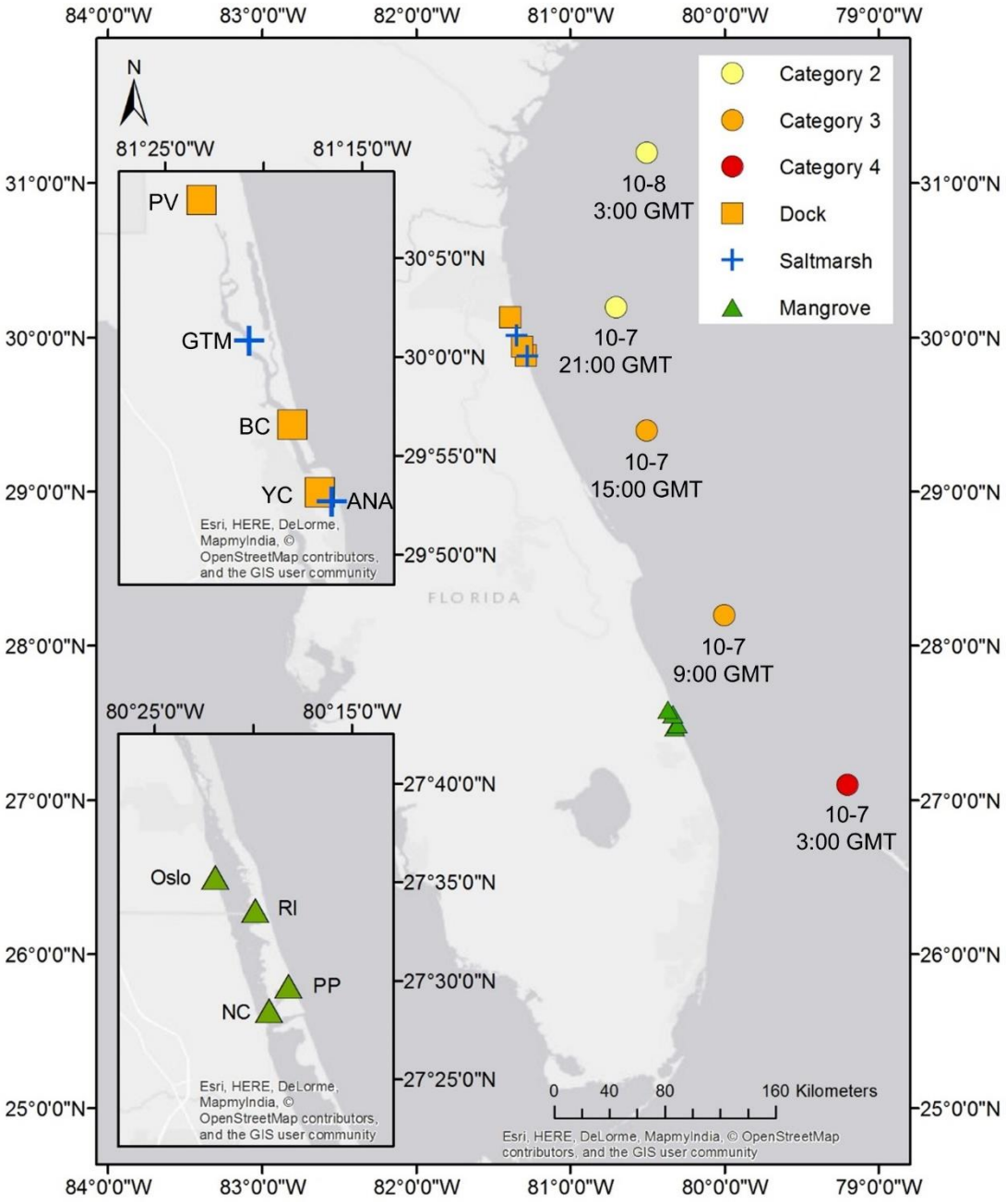

Figure 5.1. Map of study sites and the track and strength of Hurricane Matthew. Dates (Month-Day) and times (GMT) are included below the hurricane location points. The top inset shows the saltmarsh and dock sites (YC = Yacht Club; BC = Boating Club; PV = Palm Valley; ANA=Anastasia State Park; GTM = GTM NERR). The bottom inset shows the mangrove sites (NC = North Causeway Park; PP = Pepper Park; RI = Round Island Park, Oslo = Oslo Park).

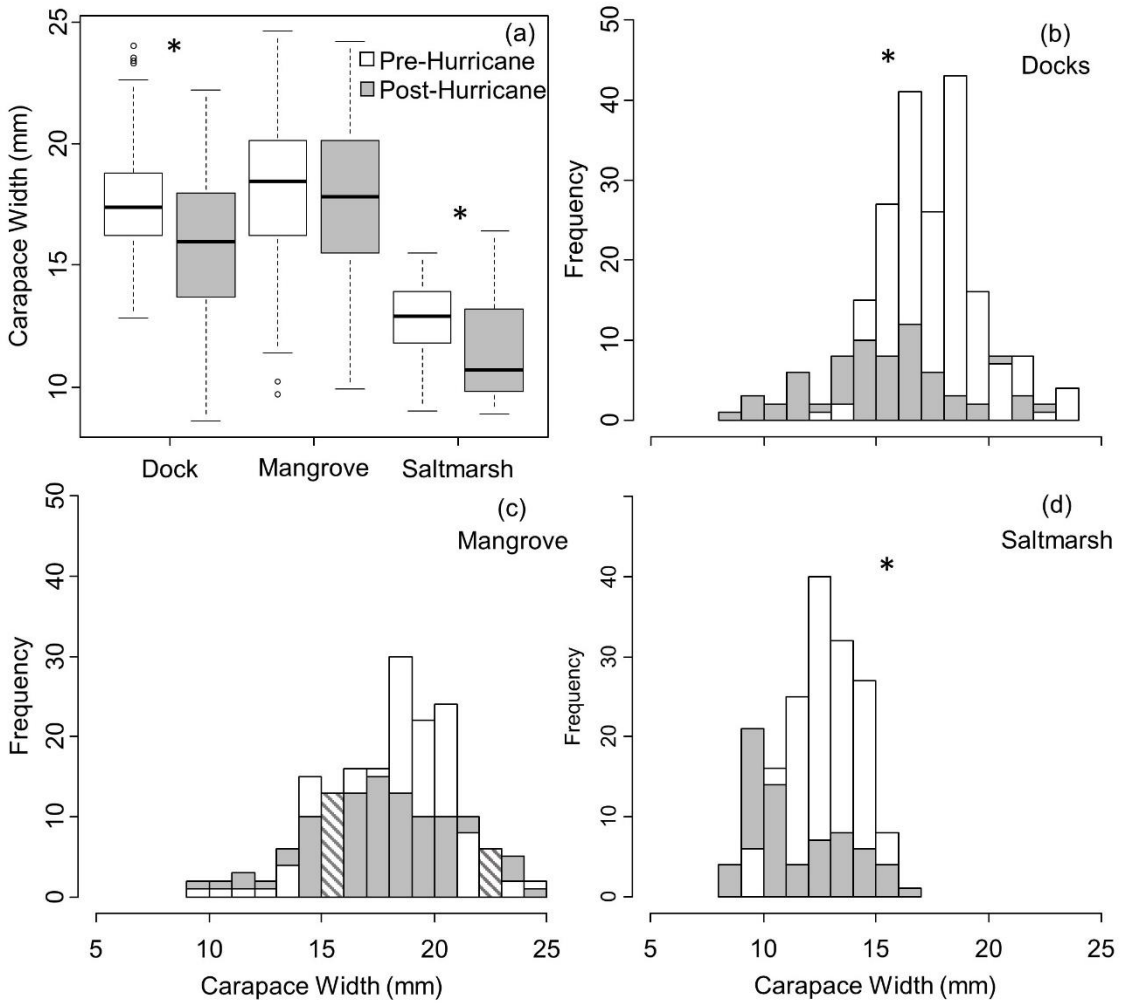

Figure 5.2. (a) Boxplots comparing the size, measured as carapace width, of *Aratus pisonii* found before and after Hurricane Matthew in the dock, mangrove, and saltmarsh habitats. Asterisks represent significant differences within habitats. In each boxplot, and in all other boxplots presented in this paper, the median is represented by a heavy line, the box represents the upper and lower quartiles, while the whiskers represent 95% of the data and circles show outliers. (b-d) Size frequency distributions of crabs found in the dock, mangrove, and saltmarsh habitats before and after Hurricane Matthew. Asterisks represent significant differences between distributions. Diagonal hatch marks in figure b represents bars of equal height pre and post hurricane.

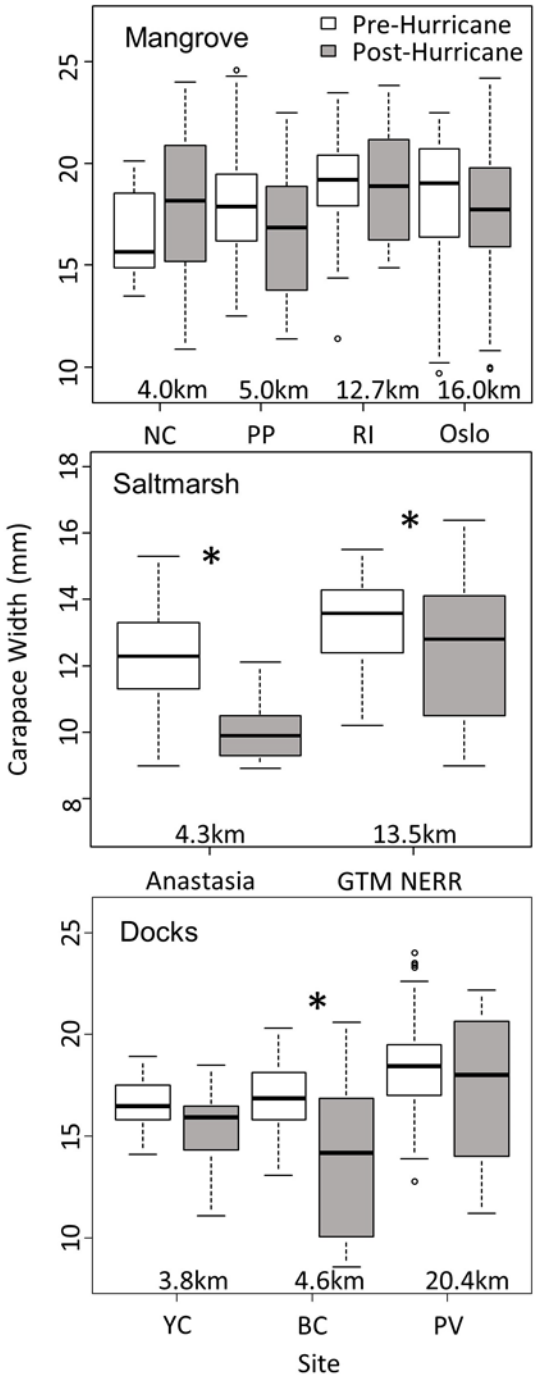

Figure 5.3. Boxplots comparing the size, measured as carapace width, of *Aratus pisonii* found before and after Hurricane Matthew within sites in the mangrove, saltmarsh, and dock habitats. NC = North Causeway Park; PP = Pepper Park; RI = Round Island Park; YC = Yacht Club; BC = Boating Club; PV = Palm Valley. Asterisks represent significant differences within sites. Distances under boxes represent the distance of that site to the nearest oceanic inlet.

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CHAPTER 6

INDIVIDUAL MORPHOLOGY AND HABITAT STRUCTURE ALTER SOCIAL INTERACTIONS IN A RANGE-SHIFTING SPECIES[1]

[1] Cannizzo ZJ, Nix SK, Whaling IC, & Griffen BD. Individual morphology and habitat structure alter social interactions in a range-shifting species. Submitted to *Diversity*

6.1 Abstract

Ecosystem engineers that serve as foundation species alter the ecology and behavior of the species which depend on them. As species shift their geographic ranges into ecosystems they have not previously inhabited, it is important to understand how interactions with novel foundation species alter their behavior. By employing behavioral assays and morphological analyses, we examined how foundation species structure and individual morphology impact the ritualistic aggression behavior of the range shifting mangrove tree crab *Aratus pisonii* between its historic and colonized habitats. Structure provided by the foundation species of the colonized salt marsh ecosystem increases the incidence and cost of this behavior over the historic mangrove habitat. Further, docks within the salt marsh, which are structurally analogous to mangroves, mitigate some, but not all, of the increased costs of performing ritualized aggression. Crabs in the salt marsh also had relatively larger claws than conspecifics from the dock and mangrove habitats, which has implications for the cost and outcomes of ritualized interactions. These changes to morphology and behavior highlight the impacts that the structure of foundation species can have on the morphology, ecology, and behavior of organisms and the importance of studying these impacts in range shifting species.

6.2 Introduction

Autogenic ecosystem engineers, organisms that change the environment or create habitat via their own physical structure (Jones et al. 1994), impact nearly every aspect of the ecology of organisms which depend on them. For those engineers which also act as ecosystem foundation species (i.e. coral in a reef, mangroves in a forest, etc.), the

ecologies of countless species have evolved to take advantage of and survive in the habitats they provide. Among the many aspects of an organism's ecology that are tied to foundation species, behavior may have one of the largest impacts on daily fitness and survival. Foundation species impact a range of behaviors from foraging in crabs (Cannizzo & Griffen 2016), birds (Bruschetti et al. 2009), and rodents (Jayadevan et al. 2018) to predator avoidance in bivalves (Gribben & Wright 2014) and fish (O'Brien et al. 2018). Such behaviors can have drastic effects on the long-term life history, ecology, and fitness of individuals and populations. However, mismatches in climate-mediated shifting rates are causing some species to decouple their geographic ranges with those of the foundation species on which they have historically depended (Schweiger et al. 2008). When this occurs, shifting species may colonize ecosystems where the foundation species differ greatly from those to which they are adapted, a phenomenon that is expected to become more frequent with continued climate change (Schweiger et al. 2008, Walther 2010). While alterations in behavior are often a first response to changing conditions (Wong & Candolin 2015), differences presented by novel foundation species, both structural and non-structural, may themselves alter ecologically important behaviors (Gribben & Wright 2014, Cannizzo & Griffen 2016). Thus, understanding how the behaviors of range shifting species are impacted by interactions with novel foundation species is vital to understanding and predicting the outcomes and impacts of range shifts.

The mangrove tree crab *Aratus pisonii* serves as an ideal model for examining the impacts of novel foundation species on behavior. The climate-mediated northward range expansion of this historically mangrove-associated arboreal crab has recently resulted in its colonization of the saltmarshes of Florida and Georgia (Riley et al. 2014). The

foundation species in the saltmarsh, the grass *Spartina alterniflora*, differs greatly in structure from mangrove trees leading to the alteration of numerous aspects of this crab's ecology, including behavior (Cannizzo & Griffen 2016, Riley & Griffen 2017, Cannizzo et al. 2018, Cannizzo et al., In Review). However, *A. pisonii* are also found on artificial boat docks within the salt marsh. Docks are more structurally similar to mangroves and mitigate many of the negative impacts this species experiences in the salt marsh, including behavioral changes (Cannizzo et al. 2018, Cannizzo et al. In Review). Docks, while not themselves a foundation species, are a result of an allogenic ecosystem engineer (humans), which provides structure similar to autogenic engineers, thus altering the flow of resources (case 4 engineering, Jones et al 1994). Thus, for the purposes of simplicity, we refer to docks as "foundation structure". This combination of historic (mangroves) and novel (marsh grass) foundation species, along with a structural analogue to the historic foundation species (docks), allows for the ability to tease apart the impacts of differing structure on ecologically relevant behaviors.

One such ecologically relevant behavior is ritualistic aggression (or ritualized combat). Like many species, *A. pisonii* males engage in ritualistic aggression following a stereotypical sequential assessment model where individuals vary their behavior during an interaction from low to high cost until a winner emerges, allowing opponents to avoid physical injury by determining the likely winner of a fight without physical confrontation (Enquist & Leimar 1983, Warner 1970). Animals use this type of behavior for a variety of vital functions, from courtship (Greene & Mason 2000, Slater et al. 2008, Thiel & Lovrich 2011) and territory defense (Schofield et al. 2007, Fernandez et al. 2014) to the establishment of social hierarchies (Mercier 1997, Skaggs et al. 2014, Trisko and Smuts

2015, Wilczynski et al. 2015). In *A. pisonii*, this behavior allows for the low-cost establishment of a social hierarchy based on size and sex that provides for effective division of resources (Warner 1970). However, as *A. pisonii* climbs structure during rising tides to avoid aquatic predation (pers. observ., Warner 1967), the structure on which the interaction occurs may determine the outcome, cost, and sequence of this behavior. In particular, the minimal surface area provided by grass stalks in the salt marsh may make performing the behavior difficult or, if crabs are more likely to fall in water, dangerous. Either could have cascading effects for the ability of the population to establish their ecologically important social hierarchy.

The differing habitats where *A. pisonii* is found could also indirectly impact this behavior through alterations to crab morphology. In *A. pisonii*, the winner of ritualized interactions is largely determined by size and, to a lesser degree, relative claw size (Warner 1970). As in many species, ornamentation or weaponry (claws) are displayed throughout the interaction with relatively larger weapons signifying a higher probability of winning a physical confrontation and thus serving as a reliable way for competitors to assess their opponents' fighting ability before engaging in a potentially costly fight (Warner 1970, Enquist & Leimar 1983, Sneddon et al. 1997). However, claw size in crabs is highly plastic (Brian et al. 2006). Many factors related to habitat type can alter claw size, including a more carnivorous diet (Smith & Palmer 1994), which *A. pisonii* experiences on docks (Cannizzo et al. 2018, Cannizzo et al In Review). Thus, differences in claw morphology between habitats must be considered to fully understand the impact of habitat structure on the ritualistic aggression behavior of this crab.

We sought to determine if the structure of foundation species impacts the ritualistic aggression behavior of male *A. pisonii*. To do so, we performed a variety of behavioral assays pitting crabs against similar-sized conspecifics originating from the same and other habitats on structures representative of each habitat. We also determined if and how claw morphology differs between habitats and, by pitting competitors from different habitats across structural types, how these morphological differences alter the ritualistic behavior and its outcomes. Ultimately, we hypothesized that both substrate structure and claw morphology would impact ritualistic aggression in *A. pisonii*. In particular, we expected that the minimal structure provided by marsh grasses would reduce the incidence of ritualized aggression but increase the cost of those interactions which do occur. Further, we hypothesized that the relatively high rate of carnivory exhibited in the dock habitat (Cannizzo et al. 2018, Cannizzo et al. In Review) would lead to relatively larger claws resulting in a higher rate of victory over conspecific from the salt marsh and mangrove habitats, and that the victor of interactions between crabs from the marsh and mangrove will not be predictable by habitat of origin.

6.3 Methods

6.3.1 Crab Collection and Preparation

While we have observed females engaging in the behavior, ritualistic aggression in *A. pisonii* is largely performed by males (Warner 1970). Thus, we exclusively examined the behavior of male crabs. All crabs were collected from either mangrove forests in and around Fort Pierce, FL or salt marsh habitat and docks in and around Saint Augustine, FL (Table 6.1). Crabs were collected by hand and placed in individual

compartments of a plastic tackle box for transport to the Smithsonian Marine Station at Fort Pierce, FL. Opaque dividers were used during transport to prevent crabs from interacting. Throughout captivity, crabs were housed in individual aquaria (22.8x15.2x16.5 cm, l x w x h) containing a petri dish of seawater and fresh food (*Rhizophora mangle* leaves), both of which were changed every other day, within a building open to ambient outdoor temperatures. Given the short time crabs were housed prior to being assayed, it is unlikely that the food provided impacted behavior. To minimize the potential impact of temperature on behavior, assays were always performed during the same time of day. Further, temperature in the building showed little day-to-day fluctuation (~2-4^{o}C) throughout the period that assays were performed. Opaque dividers were maintained between aquaria to prevent crabs from interacting. We measured the size of each crab (carapace width) to the nearest 0.1mm and painted the back of each individual with a thin stripe of one of 6 colors of nail polish for identification. Previous work has shown no effect of more extreme marking (painting of the entire carapace with nail polish) on the behavior of this species (Cannizzo et al. 2018). Crabs were then allowed to acclimate for an additional 24 hours before behavior was assayed (see below). After assaying behavior, we measured the height (CH) and length (CL) of the major claw (to the nearest 0.1mm) of each crab following the methods of de Lemos Santana et al. (2018). Crabs were returned to their site of origin within one week of assay completion.

6.3.2 Claw Morphology

To compare *A. pisonii* claw morphology between habitats, we used linear models (LM) to determine the relationships between a crab's carapace width and its CL, CH, and

CH:CL ratio. Habitat of origination was also included in the model to determine how relative claw size differed between habitats.

6.3.3 Aggression Assays

To assess how ritualistic aggression behavior was impacted by the variable influences of habitat structure and morphological differences between habitats, we ran a suite of behavioral assays. Individual crabs were only used in a single assay. Warner (1970) reported that interactions among crabs in the mangrove were most likely to occur between individuals that were similar in size. Thus, for all assays, crabs were paired with another individual that differed in size by no more than 1.3 mm and all but four interactions involved crabs that differed in size by less than 1 mm.

To understand the impact of source habitat on the ritualistic aggression behavior of *A. pisonii*, we first conducted behavioral assays in a small plastic aquarium (17.5x10.5x10 cm, l x w x h) which acted as a neutral surface (Fig. 6.1). We assayed fifteen pairs of crabs from each habitat pitting only individuals from the same habitats. To explore effects of habitat-specific differences in morphology, we also explored inter-habitat interactions in the neutral arena by performing 45 additional assays pitting individuals from different habitats (15 assays/habitat combination: dock v marsh, marsh v mangrove, mangrove v dock). For all assays, the pair of competitors were placed in the arena and allowed to interact under video recording for 10 minutes, ensuring that they were not disturbed by the presence of an observer. After each assay, crabs were returned to their respective aquaria.

We next sought to determine how the three foundation structures impacted ritual aggression behavior. Saltmarsh structure was represented by a stalk of *S. alterniflora*, mangrove structure by a mangrove prop root, and dock structure by a rounded piece of weathered wood which resembled a piling (Fig. 6.1). For each assay, the designated structure was placed in an aquarium (50.0x26.5x30.5 cm, l x w x h) with 7 cm of seawater to simulate high-tide conditions. Structures were placed to balance the desire to mimic the natural environment with the need to record both crabs throughout the assay: the grass stalk was laid diagonally across the tank while the prop root extended from the side and the dock piling was placed against the back (Fig. 6.1). For all structural assays, competitors were placed directly on the structure no more than 10 cm apart. We performed fifteen intra-habitat assays for each habitat type pitting pairs of competitors on the structure of their habitat of origin. For inter-habitat assays, we performed sixteen assays for each habitat combination. In each inter-habitat structural assay, the pair of crabs was assigned to the habitat of one competitor. For example: for the assays pitting crabs from the salt marsh with conspecifics from docks, eight pairs were assayed on marsh structure while eight interacted on dock structure. These inter-habitat structural assays allowed us to explore how interactions were impacted by the effects of habitat-specific morphological differences and crab familiarity with structural type.

After all assays were completed, we analyzed the videos using the open source video analysis software Kinovea (www.kinovea.org). We first noted if a ritualized aggression interaction occurred, defined as either crab displaying shield posturing, display, or fighting behavior (Table 6.2), and the winner of each interaction. As willingness to fight, and fight vigorously, may provide an advantage (Warner 1970, Neat

et al. 1998, Hoffman & Schildberger 2001), we noted the instigator (the first crab to perform a behavior) in each assay. Further, to explore mechanistic changes in the behavior itself, we recorded the length of the interaction, the presence/absence of each step in the ritual progression (Table 6.2), and the duration of any fighting behavior. Finally, to gain a relative measure of the danger of performing ritualistic aggression on each structure, we noted if a competitor fell in the water.

To examine the outcomes of interactions, we employed Chi-squared tests (X^2) to explore if a crab was more likely to win if it was larger, had a larger relative CL and CH, was collected from the structure type on which the assay was performed (mixed assays), or if crabs from a certain habitat type were dominant (inter-habitat assays). We used additional X^2 tests to examine if the instigator of an interaction was more likely to win, if the larger competitor was more likely to instigate, whether smaller crabs which instigated were more likely to win, and whether crabs from certain habitat types were more likely to instigate (inter-habitat assyas)

We employed a binomial general linear model (GLM) to determine which variables impacted whether an interaction occurred during the assay. The explanatory variables for this model included structural type (mangrove, salt marsh, dock, none) as well as a number of morphological characteristics of the competitors: the difference in size between competitors, the absolute sizes of the two competitors, the residuals of the relationship between relative CL and size of both crabs, the residuals of the relationship between relative CH and size of both competitors, and the difference of each of those residual values between competitors. Unless otherwise stated, these explanatory variables, in addition to interaction duration, were used in all subsequent linear models.

Residuals were used when morphological variables co-varied with crab size (LM; $p<0.05$). To gain a mechanistic understanding of how the behavior changed, we also ran binomial GLMs to determine which variables impacted whether each behavior in the behavioral progression occurred (Table 6.2), and LMs to determine which of the explanatory variables, excluding interaction duration, impacted the duration of fights and the length of the interaction. Additional binomial GLMs were also employed to determine how structure and morphology impacted the likelihood of the larger competitor winning and of a crab falling into the water (structure assays only).

All LMs and GLMs were performed using the "lme4" package in R version 3.1.1 (R core team). We then used the "step" function to determine the simplest fitted model by AIC for each LM and GLM.

6.4 Results

6.4.1 Claw morphology

All measures of claw size (CL, CH, CH:CL) increased with crab size ($p<0.001$ for each; CL: estim.=0.806, z=86.806; CH: estim.=0.587, z=64.614; CH:CL: estim.=0.013, z=64.614; Fig. 6.2). Unexpectedly crabs from the salt marsh had relatively larger claws, in all measures, than conspecifics from either the dock or mangrove habitats ($p<0.001$ for all; vs dock: CL: estim.=-0.417, z=-7.153, CH: estim.=-0.549, z=-9.640, CH:CL: estim.=-0.041, z=-8.586; vs mangrove: CL: estim.=-0.898, z=-15.113, CH: estim.=-1.020, z=-17.533, CH:CL: estim.=-0.073, z=-14.937 Fig. 6.2) while crabs from the dock habitat had relatively larger claws than conspecifics from the mangrove ($p<0.001$ for all; CL:

estim.=-0.482, z=-9.106, CH: estim.=-0.471, z=-9.109, CH:CL: estim.=-0.320, z=-7.329; Fig. 6.2), which was consistent with expectations.

6.4.2 Aggression Assays

For the purpose of simplicity, here we present only the results of those variables found to have a significant effect in the simplest model (by AIC). Foundation structure impacted a number of aspects of ritualistic aggression in *A. pisonii*. Interactions were both shorter (estim.=28.803, z=2.298, p=0.023) and less likely to occur (estim.=1.130, z=2.603, p=0.009) on dock structure than on a neutral surface. Interactions were also more likely on salt marsh structure compared to both dock (estim.=-1.618, z=-2.759, p=0.006) and mangrove structure (estim.=-1.312, z=-2.050, p=0.040). In addition to altering the occurrence of interactions, the structure on which crabs engaged in ritualized aggression impacted the behavior itself. Competitors were more likely to skip the low-cost shield posture behavior and move directly to higher cost behaviors, on dock (estim.=-2.552, z=-2.171, p=0.030), salt marsh (estim.=-2.580, z=-2.241, p=0.025), and neutral structures (estim.=-2.156, z=-1.986, p=0.047) than on mangrove structure. After a winner was determined, the winner was then less likely to display on dock structure compared to mangrove (estim.=2.131, z=2.528, p=0.012) and neutral surfaces (estim.=1.701, z=2.665, p=0.008) while the loser was more likely to retreat on mangrove structure than salt marsh (estim.=-2.805, z=-2.448, p=0.014) and neutral surfaces (estim.=-2.271, z=-2.097, p=0.036), suggesting that display may trigger this conciliatory behavior. Further, interactions were more likely to result in a competitor falling in the water, increasing the danger of the interaction, when performed on dock (estim.=-3.825, z=-3.063, p=0.002) or salt marsh structure (estim. -4.533, -3.524, p<0.001) than on

mangrove. Despite these effects, there was no advantage to individuals that were captured on the same type of structure where interactions occurred (X^2_1=0.067, p=0.414; Fig. 6.3).

Crab morphology also had numerous effects on ritualistic aggression. While morphology did not impact the length or occurrence of interactions, it altered many aspects of the ritual progression. Morphology of the smaller competitor was particularly impactful, as CL was inversely correlated with the likelihood of shield posturing (estim.=-2.438, z=-2.042, p=0.041), and body size was positively correlated with the likelihood of pre-fight displays (estim.=0.271, z=2.885, p=0.004). Further, retreat was more likely as the CH of the smaller competitor increased (estim.=1.591, z=1.970, p=0.049). In contrast, the morphology of the larger crab affected only post-interaction display, which was more likely as its body size increased (estim.=0.219, z=2.117, p=0.034). Morphology also effected the outcomes of interactions, as crabs were more likely to be victorious if they had a larger body size (X^2_1=5.828, p=0.016; Fig. 6.3), a larger relative CL (X^2_1=27.129, p<0.001; Fig. 6.3), or a larger relative CH (X^2_1=29.032, p<0.001; Fig. 6.3). The larger competitor's chances of victory also increased further as the difference in relative CL of the competitors increased (estim.=1.856, z=2.152, p=0.031). Finally, morphology impacted the cost of the behavior, as an interaction was more likely to result in a competitor falling into the water as the difference in the relative CL between competitors decreased (estim.=-2.775, z=-1.129, p=0.015).

While foundation structure and crab morphology had large effects on ritual aggression behavior and its outcomes, they were not the only factors to impact this behavior or its costs. In fact, the only factor that increased the likelihood that the costliest behavior (fighting) would occur during the ritual progression was a longer interaction

(estim.=0.022, z=2.946, p=0.003), while no measured factor impacted the duration of fighting behavior. Similarly, despite increasing the incidence of the low-cost shield posture behavior (estim.=0.022, z=2.946, p=0.035), longer interactions were more likely to be costly, as the likelihood of a competitor falling into the water increased with interaction duration (estim.=0.050, z=3.862, p<0.001). Further, inter-habitat interactions were more often won by crabs originating from the salt marsh (X^2_1=18.667, p<0.001; Fig. 6.3) while originating from the dock habitat (X^2_1=0.077, p=0.782) provided no advantage. Instigators of interactions were also more likely to win (X^2_1=12.500, p<0.001; Fig. 6.3) but instigating did not provide an advantage to smaller crabs (X^2_1=0.692, p=0.405). In addition, neither larger crabs (X^2_1=1.034, p=0.309) nor those originating from the salt marsh (X^2_1=0.032, p=0.858) or dock (X^2_1=1.485, p=0.223) were more likely to instigate.

6.5 Discussion

The differences between foundation species structure impacted *A. pisonii* ritualistic aggression behavior, its outcomes, and its costs in unexpected ways (Fig. 6.4). Despite the limited surface area they provide, interactions were more likely to occur on marsh structure than either dock or mangrove structure. Even the progression of the behavior was altered by the structure on which it was performed. Interactions on mangrove structure were more likely to include the low-cost shield posturing than other structure types where crabs progressed more quickly to higher-cost behaviors. Losing competitors were also less likely to mount a conciliatory retreat on marsh structure than mangroves, potentially increasing the possibility of reigniting the interaction. These reductions of ritual complexity and tendencies to progress more quickly to higher-cost

behaviors could increase the chance of injury and energetic cost of the interaction (Huxley 1966) thus negating some of the benefit of ritualizing aggressive behavior.

These tendencies to progress more quickly to high-cost behaviors on structure from the colonized ecosystem may reflect a difference in the cost-benefit calculation from the mangrove habitat. A competitor was more likely to fall into the water on dock and marsh structure than the mangrove, likely due in part to the decreased footing they provide (low surface area on marsh structure, vertical nature of docks). This would elevate the potential danger of an interaction by increasing the chance that one or both competitors are exposed to aquatic predation, which is also higher in the colonized ecosystem (Johnston & Smith 2018). Thus, as instigators of interactions are more likely to win independent of their size or habitat of origination, and as longer interactions are more likely to result in the loser falling into the water, the higher danger of interactions on marsh and dock structure may encourage crabs to act more aggressively in the interest of increasing their chance of victory (Neat et al. 1998, Hoffman & Schildberger 2001). While ritualistic aggression is important to the division of resources in this species, it evolved in the mangrove habitat where, like many ritualized interactions, it is relatively low-cost (Warner 1970). If the structural make-up of the colonized habitats increases these costs, it could alter the ability of this species to successfully establish a social hierarchy without significant losses.

Despite the similar danger of falling into water, docks did lower the incidence of interaction compared to marsh structure. This suggests that while the cost of interactions on dock structure is relatively high, docks provide for a greater ability of competitors to avoid aggressive interactions through avoidance and retreat (Warner 1970), an option

which may be difficult on the limited structural area of marsh grasses. The increased cost of interactions on docks relative to the mangrove may simply be a reflection of the vertical nature of this structure, which could also be experienced during interactions taking place on mangrove trunks. However, mangroves provide a higher occurrence of more complex horizontal structure (in the form of prop-roots and branches) than docks. Competitors were often observed using the complex structure of mangrove roots to retreat after an interaction or avoid confrontation altogether. This ability is drastically reduced in the dock habitat where crabs may only escape by moving around a piling which does not preclude chasing by the winner. Thus, while docks may provide improved structure for ritualized aggression over marsh grasses, they clearly do not provide a perfect analogue to the historic mangrove habitat for the purposes of maintaining this behavior.

In addition to foundation species structure, crab morphology impacted ritualized aggression interactions and their outcomes (Fig. 6.4). As has been observed in numerous species (Caldwell & Dingle 1979, Gabbanini et al. 1995, Sneddon et al. 1997), larger individuals and those with larger weaponry (claws) were more likely to win interactions. Increases in size and relative claw sizes were also associated with costlier behavioral steps (i.e. less shield posture, more display), while decreasing differences in relative claw size increased the likelihood that a competitor would fall in the water. These results fit both theory and observations in other species that the more evenly matched the competitors, the more likely an interaction is to escalate and become costly (Parker 1974, Maynard Smith & Parker 1976, Poole 1989, Smith et al. 1994). However, while the impacts of morphology on interactions were largely predictable, the differences in claw

morphology between habitats were unexpected and could have consequences for this behavior in the colonized salt marsh ecosystem.

Crabs originating from the dock habitat had relatively larger claws than conspecifics from the mangrove but the relative claw size of *A. pisonii* from in the salt marsh proper was larger still. While the large claws of crabs from docks may be explained by a diet high in animal material (Smith & Palmer 1994, Cannizzo et al. 2018), the low-quality diet *A. pisonii* experiences in the salt marsh (Cannizzo et al. 2018, Cannizzo et al. In Review) makes the mechanism behind their large claws uncertain. Larger claws may provide an advantage in grasping the limited structure of grass stalks, a problem not faced by conspecifics in other habitats. Further, the relatively small size of crabs in the salt marsh compared to the mangrove and dock habitats (Cannizzo et al. 2018) may suggest that they have a slower growth rate. If body size is more plastic than claw size, this could result in relatively larger claws. However, both these hypotheses are beyond the scope of this study. It is also possible that the observed changes to ritualized aggression are themselves driving the increase in claw size. Relatively larger claws increase the probability of winning an aggressive interaction and, despite previous assertions (Warner 1970), may be even more important than overall size (Sneddon et al. 1997). In fact, the X^2 values associated with larger-clawed competitors winning interactions were more than 5-fold higher than that associated with larger crabs winning. This suggests that for *A. pisonii*, relative claw size is far more important in determining the winner of ritualized interactions. This benefit of large claws is further visible in the tendency of crabs from the salt marsh to win inter-habitat interactions regardless of relative size, habitat of competitor, or structural type. Thus, the increase in claw size may

be a plastic response to the increased danger and prevalence of aggressive interactions in the salt marsh. If this is the case, it would signify a shift to relatively greater investment into claw growth at the expense of body size and other energetic needs. However, a full test of this hypothesis would require a complete exploration of *A. pisonii* energetics, which was beyond the scope of this study. Whether this shift in morphology is a response to or a result of the observed differences in behavior between habitats, it has implications for the ritualistic aggression behavior and the ecology of this species.

As species continue to shift into novel ecosystems, it is vital to understand how interactions with novel foundation species and other ecosystem engineers impact their behavior. The alteration of *A. pisonii* ritualized aggression, and its potential costs, highlights the drastic impact that changes to foundation species structure can have on a colonizing population. The morphological and behavioral changes observed in *A. pisonii* further demonstrate how the impacts experienced by range shifters due to novel foundation species can interact in unexpected ways. Thus, as climate-mediated colonizations of novel ecosystems become more common, it will be important to understand how multiple impacts of these colonizations interact to alter the ecology, behavior, and life history of range-shifting species.

6.6 Acknowledgments

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6.7 Tables

Table 6.1. Location and habitat of collection sites.

Habitat	Site	Lat-Long
Mangrove	Pepper Park	27°29’42”N 80°18’12”W
Mangrove	Round Island Park	27°33’33”N 80°19’53”W
Mangrove	Oslo Road	27°35’14”N 80°21’55”W
Mangrove	North Causeway	27°28’28”N 80°19’12”W
Salt marsh	GTM NERR	30°0’49”N 81°20’42”W
Salt marsh	Anastasia State Park	29°52’40”N 81°16’32”W
Salt marsh	Vilano Marsh	29°55’16’N 81°17’57”W
Dock	Palm Valley	30°07’57”N 81°23’08”W
Dock	Yacht Club	29°53’09”N 81°17’08”W
Dock	Vilano Dock	29°56’33”N 81°18’32”W

Table 6.2. Ethogram of behaviors in the *A. pisonii* ritualized aggression progression.

Behavior	Description	Progression Order	Cost-Ranking (low to high)
Shield Posture	Body held high off the substrate with claws pointed down in a shield-like manner perpendicular to structure	1	1
Pre-display	Vigorous vibration of claws followed by raising of claws from shield position in an arc above the crab and back to shield posture. May be repeated many times	2	2
Fighting	Opponents grasp chelae and push each other. A fight was considered to begin when claws touched and end when claws separated	3	3
Post-display	Display behavior performed by winner of interaction. May occur with or independently from chasing behavior	4	--
Chasing	Following an opponent that has/is retreating; performed by winning competitor	4	--
Retreating	The purposeful backing away from an opponent; performed by losing competitor	4	--

6.8 Figures

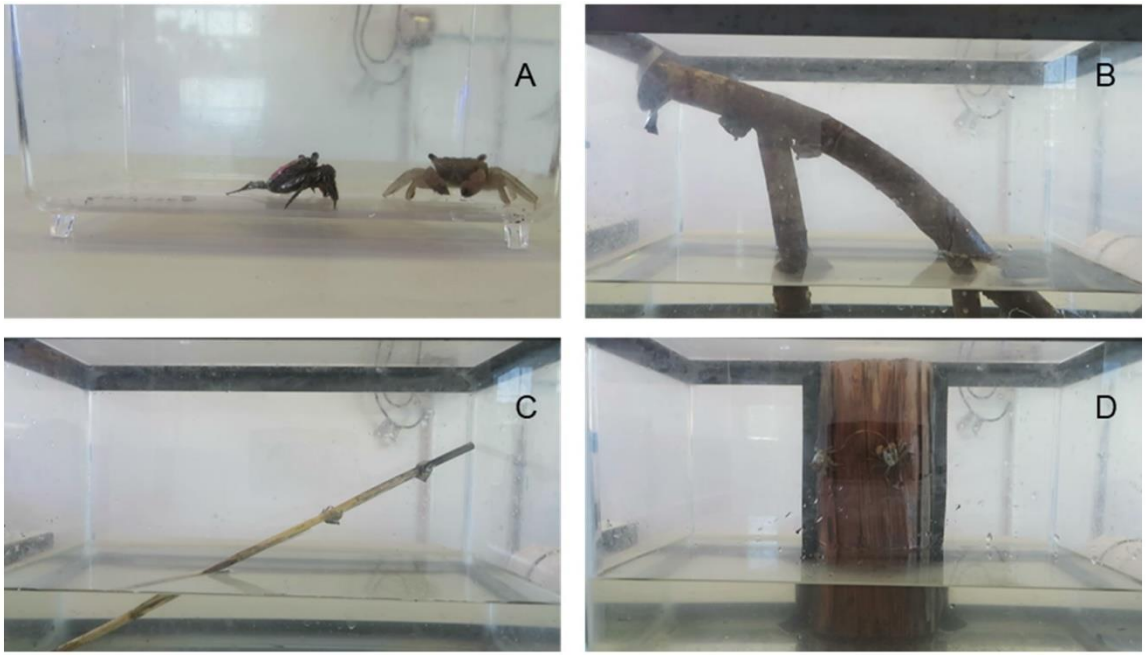


Figure 6.1. Representations of assays performed on (A) neutral structure, (B) mangrove structure, (C) salt marsh structure, and (D) dock structure.

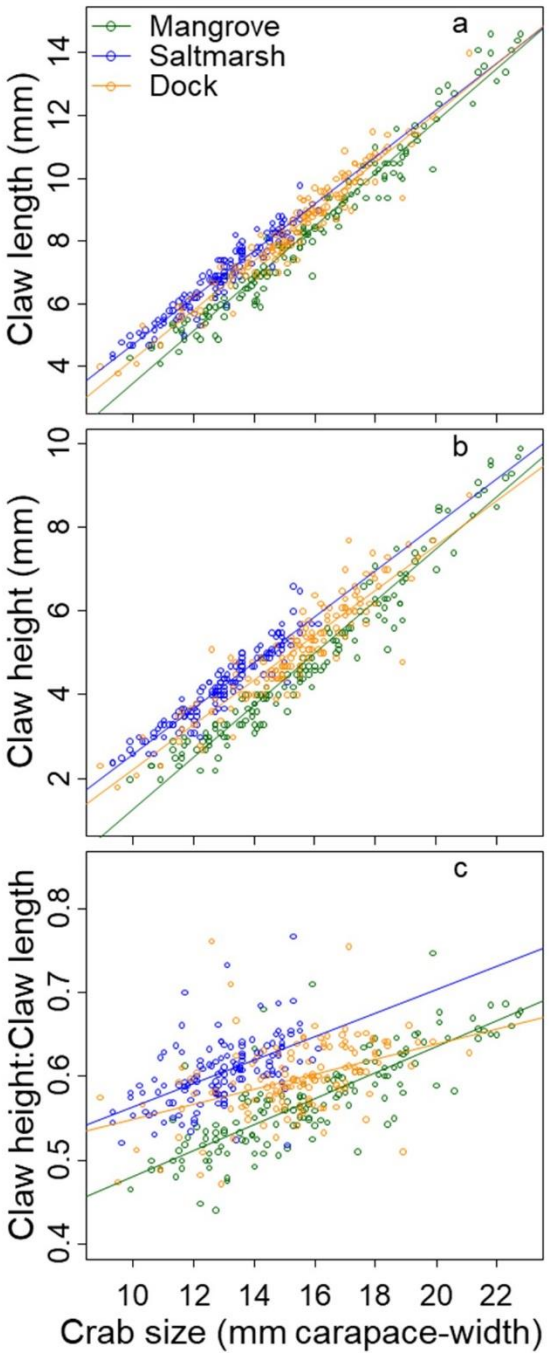


Figure 6.2. Relationships between *A. pisonii* size and (A) claw length (Mangrove: CL=0.832*body_size-4.817, adj. r^2=0.964; Salt marsh: CL=0.745* body_size-2.717, adj. r^2=0.916; Dock: CL=0.781* body_size-3.536, adj. r^2=0.928), (B) claw height (Mangrove: CL=0.620* body_size-4.932, adj. r^2= 0.947; Salt marsh: CL=0.545* body_size-2.841, adj. r^2=0.890; Dock: CL=0.534* body_size-3.123, adj. r^2=0.836), and (C) claw-height:claw-length ratio (Mangrove: CH:CL=0.015 *body_size+0.327; adj. r^2= 0.660; Salt marsh: CH:CL =0.014*body_size+0.424, adj. r^2=0.288; Dock: CH:CL =0.009*body_size+ 0.458, adj. r^2=0.173).

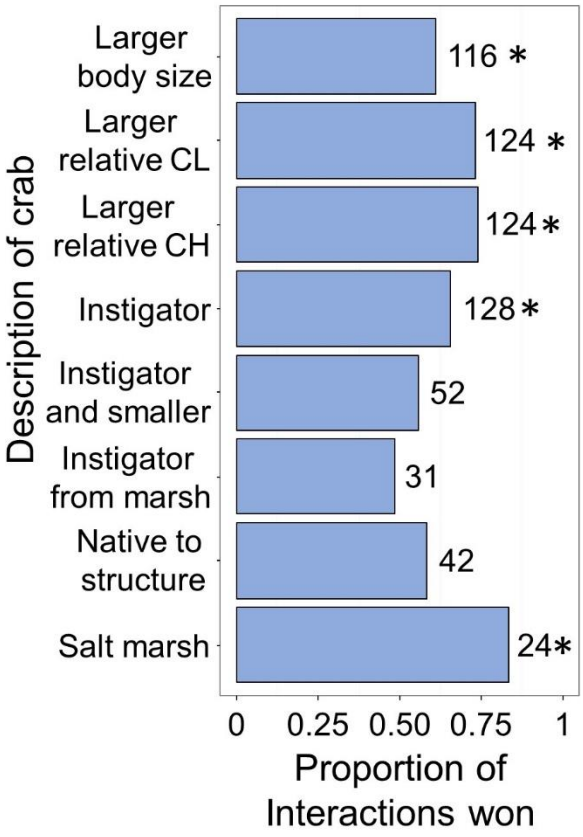
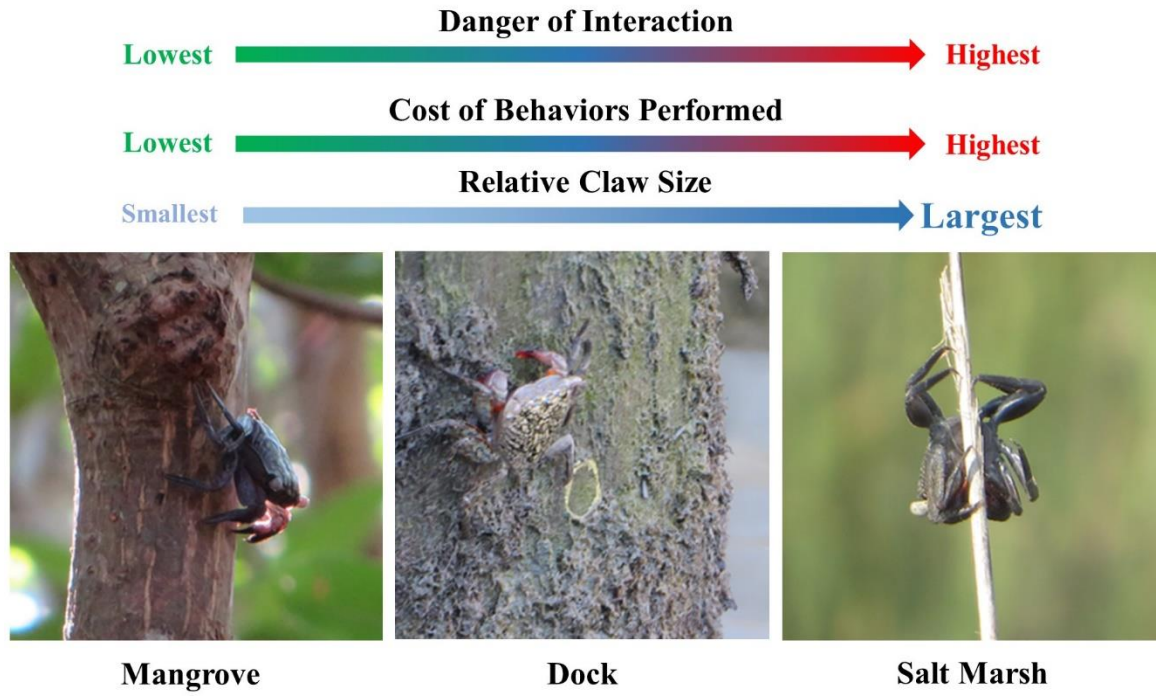


Figure 6.3. Proportion of interactions won by a variety of categories of competitor. Numbers represent the number of interactions examined while asterisks represent significant effects



	Chance of Winning
Larger Body Size	↑
Relatively Larger Claws	↑
Originating from Salt Marsh	↑
Originating from Dock	▬

Figure 6.4. Summary of the effects of foundation structure and morphology on *A. pisonii* ritualistic aggression behavior. A green arrow indicates an increase while a black das indicates no effect

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CHAPTER 7

AN ARTIFICIAL HABITAT FACILITATES A CLIMATE-MEDIATED RANGE EXPANSION INTO A SUBOPTIMAL NOVEL ECOSYSTEM[1]

[1] Cannizzo ZJ & Griffen BD. An artificial habitat facilitates a climate-mediated range expansion into a suboptimal novel ecosystem. Submitted to *PLOS One*

7.1 Abstract

As the geographic ranges of tropical species and ecosystems continue to shift poleward, it is critical to identify factors that facilitate these expansions. This is especially true for range shifts that involve the colonization of an ecosystem that the shifting species has not previously inhabited, as the factors that determine the rate of shift and survival in that ecosystem are often particularly unclear. Here we document the facilitation of the range shift of the mangrove tree crab (*Aratus pisonii*) into the colonized salt marsh ecosystem by the artificial habitat analogue of docks. We find that docks within the salt marsh act as a stepping stone refuge by providing this historically tropical species with a relatively warm thermal refuge during the winter that appears to prevent, or at least mitigate, seasonal die-backs exhibited elsewhere at the range edge. As a result, these crabs were found on docks 36 km and 22 km further north than elsewhere in the salt marsh after the winters of 2016-‘17 and ’17-’18 respectively. While artificial habitats often favor the expansion of non-indigenous species, our results represent the passive facilitation of a native species’ range shift into an ecosystem to which it is ecologically and evolutionarily naïve. The potential for analogous and refuge habitats, artificial or otherwise, to increase the rate and success of range shifts could be critical to the fate of many current and future range shifting species.

7.2 Introduction

One of the most conspicuous impacts of climate change is the worldwide shift in the geographic ranges of species and ecosystems (Walther et al. 2002, Sorte et al. 2010, Canning-Clode et al. 2011). In particular, many tropical species are expanding poleward

into temperate regions (Canning-Clode et al. 2011, Saintilan et al. 2014). The expansions of these species are often coupled with shifts of the foundation species of their historic ecosystems (Walther 2010). However, some species decouple their range shifts from those of their historic foundation species and expand at a faster rate resulting in the colonization of novel environments with which they have little or no ecological or evolutionary history (Schweiger et al. 2008). These colonized ecosystems, which are novel to the expanding species, are likely to differ from the expanding species' historic ecosystem in ways that will have consequences for its ecology, life history, and range shift.

Colonization of new ecosystems exposes species to novel biological and environmental interactions which may result in suboptimal conditions that slow further expansion (Holt et al. 2005, Keller & Taylor 2008, Riley & Griffen 2017, Cannizzo et al. 2018, Cannizzo et al. In Review). However, pockets of habitat which provide improved conditions can act as stepping stone refuges allowing species to expand through otherwise unfavorable or uninhabitable habitat. While stepping stone refuges are often thought of as corridors between favorable habitats (Thomas et al. 2001, Kramer-Schadt et al. 2011, Chester & Robson 2013), they may also increase the expansion speed and penetration into previously uninhabited ecosystems by providing refuge from suboptimal impacts or disturbances that would otherwise limit the range.

The geographic range of poleward-expanding species is often limited by winter temperatures (Walther et al. 2002, Saintilan et al. 2014). While a species may expand northward during warmer months, winter die-backs are common at the range-edge, leading to a characteristic pattern of surges and setbacks (Crozier 2004, Canning-Clode et

al. 2011, Canning-Clode & Carlton 2017). For such species, habitats that provide thermal refuge may be critical to their ability to continue to expand poleward and have even been shown to nearly eliminate latitudinal gradients in thermal stress (Jurgens & Gaylord 2018). Even minimal thermal refuge could prevent the need to recolonize each year, allowing populations to establish further north than would otherwise be possible. For example, temperatures under the canopy of stunted mangrove stands in Louisiana are about 2 ^{o}C warmer than the surrounding salt marsh leading to reduced frost damage and increased survival of recruiting mangrove seedlings (D'Odorico et al. 2013; Jiang et al. 2016). Such a canopy-like feature is rare in the salt marsh but can also be found under artificial structures such as boat docks. If these structures similarly provide thermal refuge, they may permit poleward-expanding estuarine species to survive further north than would otherwise be possible. Even a modest latitudinal effect on the range of a species could be significant to its geographic coverage if it allows for expansion into a new region, such as a river system, or beyond a dispersal barrier.

While the study of artificial habitats in range-expansions often highlights their role in facilitating invasions (Rahel 2002, Glasby et al. 2007, Sheehy & Vik 2010, Davis et al. 2014), these structures can also be beneficial to native species by acting as habitat analogues to their historic ecosystem (Santoul et al. 2009, Chester & Robson 2013) and may thus aid their range expansions. Analogous habitats, artificial habitats that resemble the historic ecosystem of a species within a suboptimal environment (*sensu* Lundholm & Richardson 2010), can provide a number of important ecological and life history benefits (Sexton et al. 2009, Cannizzo et al. 2018, Cannizzo et al. In Review) and offer refuge from environmental impacts (Cannizzo & Griffen 2018, Cannizzo et al. 2018). For

example, boat docks act as an analogous habitat for the mangrove tree crab *Aratus pisonii* within colonized salt marshes. This historically Neotropical mangrove associated crab (Rathbun 1918, Warner 1967, Beever et al. 1979) has recently outpaced the northern range expansion of mangroves and colonized saltmarshes on the Southern US Atlantic coast (Riley et al. 2014). Crabs in the salt marsh experience inferior thermal and foraging conditions (Cannizzo et al. 2018) and exhibit altered behavior (Cannizzo & Griffen 2016, Cannizzo et al. 2018), smaller size (Riley & Griffen 2017, Cannizzo et al. 2018), and reduced larval quality (Riley & Griffen 2017, Cannizzo et al. In Review) compared to conspecifics in the mangrove. Docks mitigate many of these impacts by providing improved thermal and foraging conditions resulting in increased reproductive fitness (Cannizzo et al. 2018, Cannizzo et al. In Review). If docks allow *A. pisonii* to expand northward more quickly, or survive further north than would otherwise be possible, they could play a critical role in determining the rate of this species' expansion and the ultimate outcome of this range shift.

Here we examine the impact of docks on the range expansion of *A. pisonii* through distributional surveys and measures relevant to individual and population survival: cold tolerance and abundance. We hypothesize that *A. pisonii* will be found further north on docks within the salt marsh than in the salt marsh proper. Further, we predict that docks will provide a critical thermal buffer during cold periods resulting in smaller geographical winter die-backs than elsewhere at the range-edge.

7.3 Methods

7.3.1 Distributional Surveys

To determine the northern extent of the range of *A. pisonii* in the salt marsh and on docks, and the extent to which those distributions changed after winter die-backs, we conducted distributional surveys at the northern edge of the crab's range in the autumns and following springs of two consecutive years. We conducted our autumn surveys during the last week of November in 2016 and 2017. As *A. pisonii* largely stops reproducing in October (Cannizzo et al. In Review), this allowed us to record the furthest Northward extent of the species each year. The most recent survey of the geographical range of *A. pisonii* was undertaken in 2013 (Riley et al. 2014) and cited the northern extent as Little Satilla Creek, Georgia (31º5'32"N) with no individuals found just south at Jekyll Island, Georgia (31º2'31"N). Thus, we began our autumn 2016 survey at Jekyll Island and moved north along the coast until we encountered two consecutive sites where no *A. pisonii* were found (Table 7.1). Sites were selected based on accessibility and access to both salt marsh and dock habitat via kayak. In all habitats, the largely terrestrial *A. pisonii* climbs structure to avoid rising waters and aquatic predation (pers. observ., Warner1967, Wilson 1989). Therefore, we always conducted surveys during tidal inundation of the salt marsh to increase the likelihood that if *A. pisonii* were present, they would be found climbing marsh grasses.

While the presence-absence of individuals is an important measure of the geographic extent of a species, the establishment of a reproductive population is of particular importance to its long-term persistence in a newly colonized location. Thus, we

chose to conduct the spring surveys during the week before the full moon of May 2017 and the week before the new moon of June 2018. This allowed us to take advantage of the lunar synchronization of *A. pisonii* reproduction (Warner 1967) by conducting surveys during, or shortly after, the first reproductive cycle of the breeding season (Cannizzo et al. In Review) ensuring that any individual encountered had overwintered at the sites where they were found. While logistical constraints caused a delay in the spring 2018 survey, the survey was conducted less than 2 weeks after the first reproductive cycle. Given the ~20-day planktonic stage of *A. pisonii* larvae (Warner 1967), any crabs found were unlikely to have been recent recruits. Further, we did not encounter any crabs below reproductive size in this survey ensuring that the observed crabs had survived the winter at the site where they were found. We conducted the spring surveys using the same methods as the autumn surveys and noted the presence or absence of ovigerous (egg carrying) females at each site.

During the first survey year (2016-2017), we captured 15 crabs, or all that were found, at each site and recorded the sex and size (measured as carapace width to the nearest 0.1mm) of each individual. For the spring surveys, size data were compared to the smallest and average sizes of ovigerous females recorded from each habitat in areas where *A. pisonii* is established (Cannizzo et al. In Review). A similar strategy was employed in the second survey year (2017-2018) with catch effort added to gain a measure of relative abundance (see below).

During each survey after the autumn of 2016, we sequentially added additional sites to more accurately pin-point the northern location of *A. pisonii*. This resulted in the addition of Village Creek in the spring of 2017, Halfmoon Marina and Sunbury Boat

Ramp in the autumn of 2017, and three sites in the spring of 2018: Big Talbot Island, Fernandina Beach, and Crooked River (Table 7.1).

7.3.2 Relative abundance

During the second survey year, we sought to measure the relative abundance of *A. pisonii* in each habitat at each site as catch per unit effort (CPUE) in crabs caught per minute. The sex and size of each captured crab was also recorded as described above. This measure was intended to allow for both a relative measure of the reduction of abundance after a winter die-back and the identification of an expansion front. In spring 2018, we also explored population abundances in three dock and three salt marsh sites that have been inhabited by *A. pisonii* for more than a decade allowing for a comparison of abundance in edge and established populations. For the 2017-2018 survey year, we explored population abundance using a linear model with latitude, habitat, season (spring/autumn), and level of establishment (edge/established) as explanatory variables. As established populations were not sampled in the autumn, a similar model was also used for data from the spring survey only to compare edge and established populations.

7.3.3 Cold Tolerance

To fully understand the extent to which docks may act as a thermal refuge we sought to determine the cold tolerance of *A. pisonii*. To do so, we collected 30 crabs from each habitat and determined the size and sex of each individual before placing it in a plastic aquarium (22.8x15.2x16.5 cm, l x w x h) with food (fresh red mangrove *Rhizophora mangle* leaves) and a petri dish of water inside an incubator maintained at a 12:12 light-dark cycle for the duration of the experiment. Water was changed every other

day with fresh food given *ad libitum*. Crabs were allowed to acclimate to incubator conditions at 25 ^{o}C for 48 hours after which the temperature was linearly and gradually decreased to 20 ^{o}C over a 12-hour period. After 36 hours, the temperature was again decreased linearly over 12 hours to 15 ^{o}C. Following a further 36-hour acclimation period, the experimental program was initiated. As terrestrial organisms often experience short nightly bursts of cold temperatures with warming during the day, which could be critical to poikilothermic organisms such as *A. pisonii*, we created a temperature program that mimicked a daily cooling and warming cycle. This program began at the beginning of the dark cycle with an 11-hour linear decrease to the target temperature. The target temperature was then held for one hour until the beginning of the light cycle at which time the temperature it was increased linearly to 15 ^{o}C over a 6-hour period, where it was maintained until the next dark cycle. The target temperature on the first night was set to 14 ^{o}C and was decreased by 1 ^{o}C with each subsequent night. Crab mortality was checked each day after the program had leveled to 15 ^{o}C. Once all crabs had died, we corrected the temperatures crabs experienced with data gathered from thermal loggers placed throughout the incubator during the experiment (to account for slight spatial differences in temperature within the incubator) and examined cold-tolerance using a cox proportional hazards model with habitat, sex, and crab size as explanatory variables for the number of days survived. The proportional hazards assumption was met as Schoenfeld residuals were independent of time both globally and for all covariates ($p>0.10$). We further determined the median lethal temperature (LT50) and complete lethal temperature (LT100) of *A. pisonii* overall and for each habitat.

7.3.4 Temperature Measurements

To determine if docks provide a thermal refuge during the winter, we placed 4 Onset (Bourne, Massachusetts, USA) HOBO thermal data loggers (2 under a dock and 2 in the nearby salt marsh) at each of 4 sites (Table 7.1) which spanned the autumn 2017 range-edge. The loggers recorded temperature simultaneously every 10 minutes from December 11, 2017 to April 30, 2018. The average of the two loggers deployed in each habitat was used to calculate the temperature for that habitat at that site at 10 minute intervals. We then used habitat type and site location (in degrees latitude) as explanatory variables in a linear model to explore their effects on the number of days with at least one continuous hour below *A. pisonii* LT50 and LT100 (separate models). Similar models were used to explore the effects of habitat and latitude on the total time, in hours, spent below each threshold. In addition, we determined the daily minimum temperature recorded in each habitat at each site and employed a liner model to determine if latitude and habitat impacted the average minimum temperature experienced over the duration of the deployment. Water temperature data were also retrieved from USGS climate station 22035975, Hudson Creek, which is located at the Sapelo Island site.

While the loggers were deployed, the southeastern United States experienced an unusually cold winter. Thus, we retrieved 1988-2018 temperature data from the University of Georgia Marine Institute on Sapelo Island, Georgia, located only 10km from the Sapelo Island site. To determine if the winter of 2017-2018 truly represented an extreme cold event, we adapted the definition of an extreme event from Canning-Clode and Carlton (2017) as a period of five consecutive days with the minimum temperature below the 10^{th} percentile of daily minimum temperatures drawn from a baseline of the

past 30 winters (December-March). We also used the dataset to determine if there were any particularly extreme events where the minimum temperature remained below the 5th percentile for five consecutive days.

7.4 Results

7.4.1 Distributional Surveys

In the autumn 2016 survey, *A. pisonii* were found 4.65 minutes of latitude (~9 km) further north on docks than in the salt marsh (Table 7.1, Fig 7.1). Further, *A. pisonii* were found 21.68 minutes of latitude (~40 km) further north than in the 2013 survey (Riley et al., 2014; Table 7.1, Fig 7.1). The following spring 2017 survey revealed that the range of *A. pisonii* in the salt marsh had contracted south 14.90 minutes of latitude (~28 km) over the winter (Table 7.1, Fig 7.1). However, there was no change in the range of *A. pisonii* on docks. Thus, there was a 19.55 minute of latitude (~36 km) difference between the northernmost established population of *A. pisonii* on docks and in the saltmarsh. Further, during the spring survey ovigerous females were found in the salt marsh at all sites where crabs where found, while ovigerous females on docks were found at all but the two northernmost sites (Table 7.1). While no ovigerous females were found on the docks at Sapelo Island NERR, there were a number of females large enough to be mature and were thus likely reproductive but not ovigerous at the time of survey due to the relatively low reproductive activity of *A. pisonii* in May (Cannizzo et al. In Review).

The autumn 2017 survey revealed that *A. pisonii* had expanded northward 5.41 minutes of latitude (~10 km) from the previous northernmost location during the summer; 31.75 minutes of latitude (~59 km) further north than the 2013 survey (Riley et al. 2014,

Table 7.1, Fig. 7.1). While numerous crabs were found on docks at this location, only one juvenile male (7.5 mm) was found in the salt marsh, likely representing a recent colonization. The nearest location where we found a mature crab in the salt marsh was 10.07 minutes of latitude (~19 km) to the south (Table 7.1). Between the autumn 2017 and spring 2018 surveys, the Southeastern US experienced one of the coldest winters of the past 30 years (see below). This resulted in an extreme die-back of *A. pisonii* with the northern extent retreating 34.76 minutes of latitude (~64 km) on docks and 46.56 minutes of latitude (~86 km) in the salt marsh resulting in a loss of 3.01 and 14.80 minutes of latitude from docks and salt marsh respectively from the range-edge recorded in 2013 (Riley et al., 2014; Table 7.1, Fig. 7.1). However, *A. pisonii* were still found 11.79 minutes of latitude (~22 km) further north on docks than in the salt marsh proper.

At the time of writing, the northernmost non-seasonal extent of *A. pisonii* is Jekyll Island (31°2'31"N; Table 7.1) with two individuals found on a dock in the spring of 2018. Using the 1918 northern extent of Miami (25°48'N; Rathbun 1918), we can update the rate of *A. pisonii* range expansion to 58 km/decade, which is slower than both the 72 km/decade average rate of marine range expansions (Poloczanska et al. 2013) and the previous estimate of 62 km/decade for this species (Riley et al. 2014). Further, the estimate, if calculated from the 2016-2017 survey alone, would have been 64 km/decade highlighting the importance of encompassing extreme events and setbacks when determining rates of geographic range-shifts.

7.4.2 Relative abundance

The relative abundance of *A. pisonii* was higher on docks that in the nearby salt marsh (LM: z_{25}=-2.603, estim.=-0.683, p=0.015; Fig. 7.2) and decreased both from autumn to spring (LM: z_{25}=-3.485, estim.=-1.789, p=0.002) and with increasing latitude (LM: z_{25}=-2.763, estim.=-1.779, p=0.011). The relative abundances were numerically higher in the established populations of both habitats during the spring survey (Fig. 7.2) but this difference was not statistically significant (LM: z_{10}=-1.291, estim.=-0.440, p=0.226). While the drastic die-back of *A. pisonii* prevented direct comparisons of abundance between the autumn and spring in individual sites, the one site where crabs were found on docks in both surveys (Jekyll Island) experienced a greater than 61-fold decrease in abundance, highlighting the devastating impact of the extreme winter among even those populations that were not eliminated.

7.4.3 Cold Tolerance

The overall LT50 for *A. pisonii* was 6 ^{o}C with an LD100 of 4 ^{o}C. When habitats are examined independently, these values are the same for crabs from the mangrove and dock habitats but slightly warmer for crabs from the salt marsh (LT50 = 7 ^{o}C, LT100 = 5 ^{o}C). Despite the slightly warmer lethal temperatures for salt marsh crabs, there was no effect of habitat on crab survival (Cox PH: dock vs. mangrove: z=0.414, p=0.679; dock vs. salt marsh: z=1.741, p=0.082; mangrove vs. salt marsh: z=1.513, p=0.130; Fig. 7.3), which was also independent of sex (Cox PH: z=0.776, p=0.438) and size (Cox PH: z=0.597, p=0.551).

7.4.4 Temperature Measurements

Nighttime temperatures under docks were constantly 2-5 ^{o}C warmer than in the nearby saltmarsh but did drop below *A. pisonii* cold tolerance at even the southernmost site where loggers were deployed (Fig. 7.4). Docks also appear to generally act as a temperature buffer exhibiting lower daytime temperatures and less extreme temperature swings than in the salt marsh proper. In addition, the water temperature at Sapelo Island was often warmer than the nightly air temperatures experienced in either the salt marsh or dock habitats (Fig. 7.4a).

Compared to the dock habitat, the salt marsh experienced more days where the temperature stayed below both the LT50 and LT100 of *A. pisonii* for at least an hour (LM: LT50: z_5=4.165 estim.=17.750, p=0.009; LT100: z_5=5.202, estim.=17.000, p=0.003; Fig. 7.4b). Further, while sites further north experienced more days under the LT100 threshold (LM: z_5=2.743, estim.=19.219, p=0.041; Fig. 7.4b), the latitudinal location of sites did not impact the number of days below the LT50 threshold (LM: z_5=1.804, estim.=16.480, p=0.131; Fig. 7.4b). Similarly, the total time spent below LT50 and LT100 was higher in the salt marsh (LM: LT50: z_5=3.314, estim.=146.38, p=0.021; LT100: z_5=3.382, estim.=106.88, p=0.020; Fig. 7.4c). However, only the total time under LT100 increased with latitude (LM: LT50: z_5=1.881, estim.=178.11, p=0.119; LT100: z_5=2.794, estim.=189.32, p=0.0383 Fig. 7.4c). In addition to the lethal temperature thresholds, the daily minimums were both colder in the salt marsh (LM: z_{1125}=-7.681, estim.=-2.718, p<0.001; Fig 7.4d-e) and decreased with increasing latitude (LM: z_{1125}=-2.781, estim.=-2.109, p=0.006; Fig. 7.4d-e).

The 10th percentile of minimum winter temperatures, based on a baseline of the previous 30 winters retrieved from the Sapelo Island climate station (see above), was 0.6 ºC while the 5th percentile was -1.7 ºC. Using these values, we determined that the winter of 2017-2018 represented a cold extreme with an extreme event from January 1-7 during which a particularly extreme event also occurred from January 2-6.

7.5 Discussion

We have shown that an artificial habitat passively facilitates the range shift of a native species into a natural ecosystem that it has not previously inhabited. This passive anthropogenic facilitation of a range shift differs from that often seen in species invasions where species are often first actively transported to a new geographic location before they can expand under their own power. In contrast, *A. pisonii* has expanded out of its historic range largely without anthropogenic aid. This is not an entirely unknown phenomenon as artificial feeders and urban rubble have been shown to facilitate the range expansions of Anna's humming bird and the black redstart respectively (Grant 2006, Grieg et al. 2017). However, unlike in this study, these birds did not colonize ecosystems which were ecologically and evolutionarily novel, but merely expanded their geographic and seasonal extents within previously inhabited ecosystems.

While extreme cold events are known to cause setbacks to the range expansions of tropical species (ex: Canning-Clode et al. 2011), we have shown that artificial habitats can mitigate these impacts. Our results suggest that the artificial dock habitat acts as both a habitat analogue and a stepping-stone refuge by allowing *A. pisonii* to establish populations further north and expand more rapidly into the colonized salt marsh

ecosystem than would otherwise be possible. By acting as a thermal refuge, docks prevent, or at least mitigate, the winter die-back of seasonal populations seen elsewhere in the salt marsh ecosystem. The 2-5 ^{o}C warmer conditions under docks during cold nights can be the difference between life and death, as seen in other tropical range expanding species such as mangroves (Jiang et al. 2016). A single cold night can kill-off a seasonal population and docks appear to provide the thermal refuge that *A. pisonii* needs to survive, potentially expanding the geographical extent of the climatic envelope of the species. Recognizing this ability of artificial habitats to expand climatic envelopes (i.e. alter the physiological tolerability of an environment) could be critical to the accurate parameterization of mechanistic species distribution models used to predict range shift outcomes (Kearny & Porter 2009).

Despite the warmer conditions under docks, temperatures did drop below the apparent cold-tolerance of *A. pisonii* in both the dock and marsh; particularly during the extreme cold event from January 1-7, 2018. Yet, in the dock habitat some individuals survived at the southernmost site where thermal loggers were deployed. The survivors may have sheltered in microhabitats that were warmed during the day or retreated into the water, which stayed above the thermal minimum of *A. pisonii*. The ability to retreat to warmer water is another possible benefit provided by docks as most remain partially submerged throughout the tidal cycle. In contrast, crabs facing extreme cold during low-tide in the salt marsh are left with few if any thermal refuges (though they could feasibly utilize fiddler crab burrows). If crabs do find thermal shelter in the water, a strategy used to limit overheating in the summer (Cannizzo et al. 2018), they could still experience increased mortality as aquatic predation on *A. pisonii* is high, particularly in the salt

marsh (Johnston & Smith 2018). Thus, even if crabs in the marsh can retreat to warmer water, the warmer aerial conditions under docks likely force this retreat less often, reducing secondary impacts of predation.

By providing thermal refuge during the critical cool nights of winter, docks have the potential to act as a stepping stone refuge and increase the rate of *A. pisonii* geographic expansion over what would otherwise be possible. Simply the ability to survive further north on docks increases the penetration of this species' range into estuaries and river systems where it would not otherwise be found. Ovigerous females, or at least females of reproductive size, were found on docks at all sites in spring 2018 and all but the furthest northward site in spring 2017. Docks therefore prevent the need to reestablish every spring by providing a stock of reproductively mature crabs. As *A. pisonii* depends on larval dispersal and produces more, higher quality larvae on docks (Cannizzo et al. In Review), the ability of the population to reproduce at sites further north has the potential to accelerate the range expansion of this species. However, even if mature individuals survive the winter, they must find a mate. While *A. pisonii* relative abundance decreased with latitude and fell during the winter in both habitats, it was consistently lower in the salt marsh in range-edge populations. Thus, even if some individuals survive extreme cold events in the salt marsh, the population may face an Allee effect until re-colonization from docks or more southern populations can replenish the breeding stock, a common problem faced by range-edge populations (Chuang & Peterson 2016 and references therein). In contrast, populations on docks are more densely populated, potentially reducing any post-winter Allee effect. Further, the reversal from higher relative abundances in the salt marsh in the established range to the dock at the

range-edge may reflect either greater die-backs in range-edge marshes or preferential establishment on docks. Either would result in docks decreasing Allee effects and increasing expansion and colonization.

Ultimately, this work represents a little-studied aspect of range-shift ecology: the ability of an artificial habitat analogue to act as a stepping stone refuge and accelerate the rate of a range-shift, or at least the geographical penetration, of a native species into an ecosystem to which it is ecologically and evolutionarily naïve. There have been several discussions of the use of artificial habitats or habitat modifications to minimize the impacts of climate change on species in their historic ecosystems (Williams et al. 2008, Shoo et al. 2011). However, while many of these proposals focus on creating more favorable microhabitats (Webb & Shine 2000, Souter et al. 2004, Shoo et al. 2011), there has been little discussion of the use of artificial habitats to provide refuge in novel ecosystems (but see Cannizzo et al. 2018, Cannizzo & Griffen 2018). Further, while there has been robust discussion of the use of corridors and stepping stones to aid range shifts between favorable habitats (Hannah 2001, Krosby et al. 2010), their role in facilitating penetration into novel ecosystems has largely been contained to discussions of species invasions (Rahel 2002, Glasby et al. 2007, Davis et al. 2014). In fact, the discussion of anthropogenic habitats within range shift ecology largely focuses on the impediment they impose to native shifting species (Warren et al. 2001, Robillard et al. 2015, Gilchrist et al. 2016). However, this study highlights the role that artificial structures can play in facilitating the range-expansions of native species, a topic beginning to gain attention (Grieg et al. 2017). In fact, artificial structures can provide critical refuge habitat that not

only increases the permeability of the habitat matrix during range shifts but may accelerate the range shift itself.

As the number of species shifting their geographic ranges increases, deciphering the factors that impact shifting rates will be critical to understanding, predicting and managing outcomes. Artificial habitats have the potential to provide refuge from suboptimal novel conditions allowing species to shift more rapidly and more deeply into colonized ecosystems than would otherwise be possible. Thus, this study supplements work on expansions of non-indigenous species by highlighting the critical role that artificial stepping stone and analogous habitats can play in the range expansions of native species into novel ecosystems. Ultimately, the potential of analogous and refuge habitats, artificial or otherwise, to increase the rate and success of range shifts could be critical to the fate of many current and future range shifting species.

7.6 Acknowledgments

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7.7 Tables

Table 7.1. Site locations, presence (Y) and absence (N) of *A. pisonii* and ovigerous/mature females, presence of *A. pisonii* in 2013 survey (Riley et al., 2014). Asterisks denote sites of thermal logger deployment.

Site	Lat.-Long.	Salt marsh autumn 2016	Salt marsh Spring 2017 (Ovigerous/ Mature)	Dock autumn 2016	Dock Spring 2017 (Ovigerous/ Mature)	Salt marsh autumn 2017	Salt marsh Spring 2018 (Ovigerous/ Mature)	Dock autumn 2017	Dock Spring 2018 (Ovigerous/ Mature)	Riley et al.
Sunbury Boat Ramp	31°45'51"N 81°16'41"W	--	--	--	--	N	N	N	N	--
Halfmoon Marina	31°41'42"N 81°16'17"W	--	--	--	--	N	N	N	N	--
Barbour River	31°37'17"N 81°15'49"W	N	N	N	N	Y	N	Y	N	--
Dallas Bluff *	31°35'25"N 81°18'8"W	N	N	N	N	N	N	Y	N	--
Belleville Launch	31°31'52"N 81°21'32"	N	N	Y	Y (N/N)	N	N	Y	N	--
Sapelo Island NERR *	31°27'13"N 81°21'46"W	Y	N	Y	Y (N/Y)	Y	N	Y	N	--
Blue N. Hall Landing	31°24'21"N 81°23'33"W	Y	N	Y	Y (Y)	Y	N	Y	N	--
Village Creek	31°12'19"N 81°21'36"W	--	Y (Y)	--	Y (Y)	Y	N	Y	N	--
Little Satilla River *	31°5'32"N 81°34'15"W	Y	N	Y	Y (Y)	Y	N	Y	N	Y
Jekyll Island *	31°2'31"N 81°25'21"W	Y	Y (Y)	Y	Y (Y)	Y	N	Y	Y (N/Y)	N
Crooked River	30°50'44"N 81°33'34"W	--	--	--	--	--	Y (N/Y)	--	Y (Y)	Y
Fernandina Beach	30°40'16"N 81°27'56"W	--	--	--	--	--	Y (N/Y)	--	Y (Y)	Y
Big Talbot State Park	30°22'30"N 81°35'6"W	--	--	--	--	--	Y (N/A)	--	Y (Y)	Y

7.8 Figures

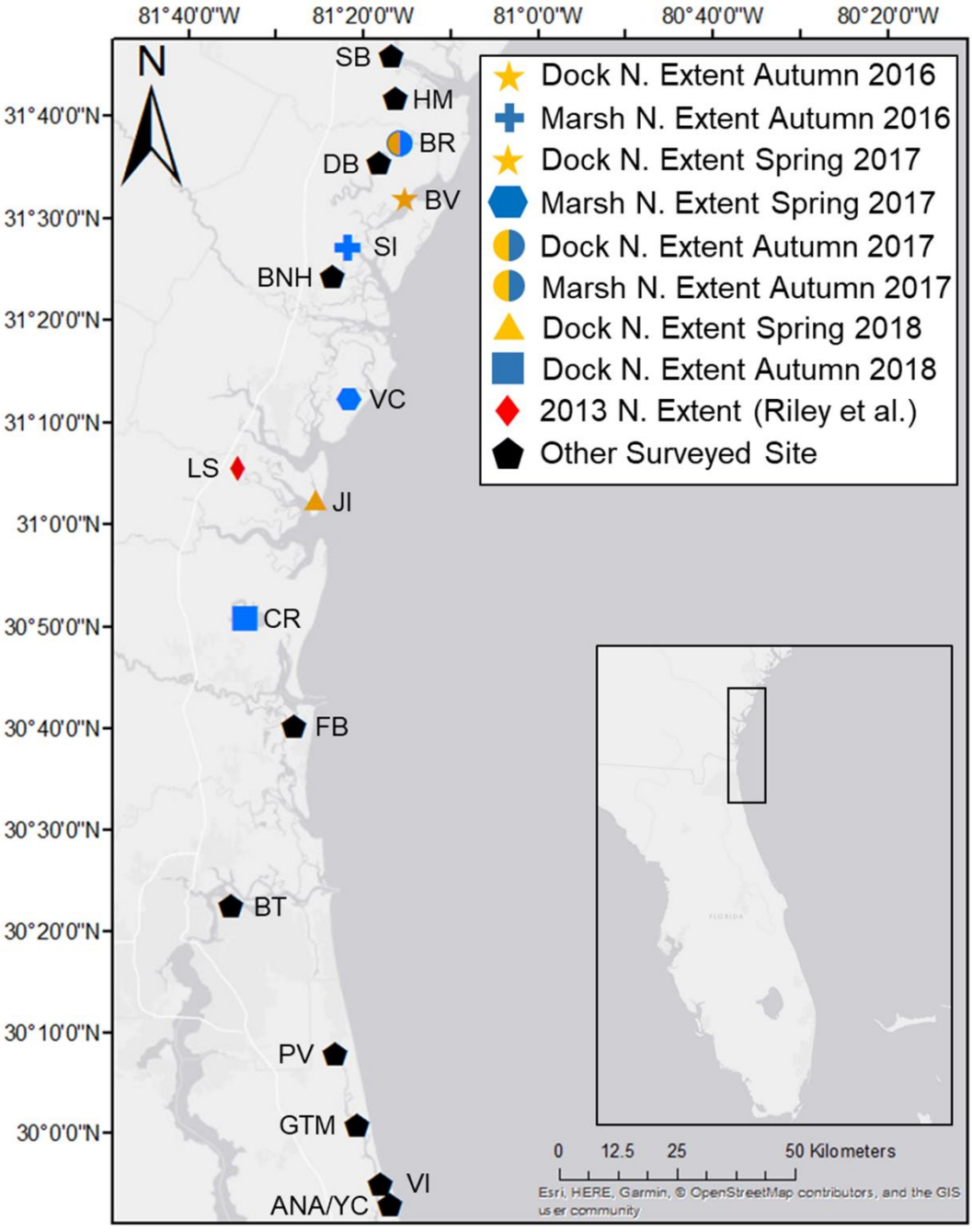

Figure 7.1. Map of survey sites. Top to bottom: SB = Sunbury Boat Ramp, HM = Half Moon Marina, BR = Barbour River, DB = Dallas Bluff, BV = Belleville Launch, SI = Sapelo Island NERR, BNH = Blue N Hall Landing, VC = Village Creek, LS = Little Satilla Creek, JI = Jekyll Island, CR = Crooked River, FB = Fernandina Beach, BT = Big Talbot State Park, PV = Palm Valley, GTM = GTM NERR, VI = Vilano Inlet, ANA/YC = Anastasia State Park/Yacht Club. Both dock and salt marsh habitat were surveyed at all sites with the exception of PV (dock only) and GTM (marsh only). Inset displays map location.

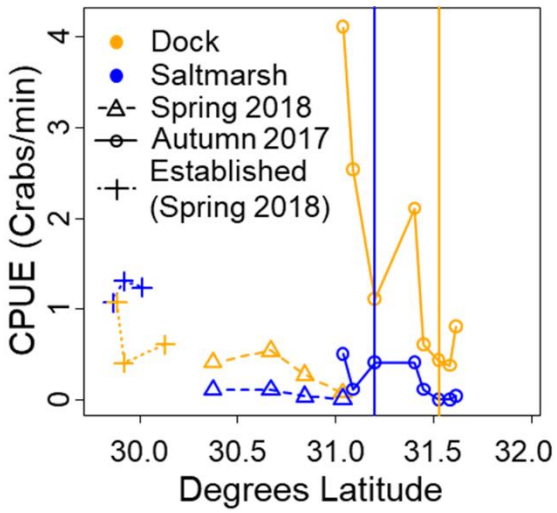

Figure 7.2. *A. pisonii* density as catch per unit effort (CPUE) in the salt marsh and on docks of sites surveyed during the 2017-2018 surveys and three sites per habitat in the established range, surveyed Spring 2018. Vertical blue and orange lines represent the northern extent of *A. pisonii* as of the Spring 2017 survey in the salt marsh and dock habitats respectively. Lack of autumn 2017 data south of 31^{o} N signifies no sampling of these sites during the autumn 2017 survey.

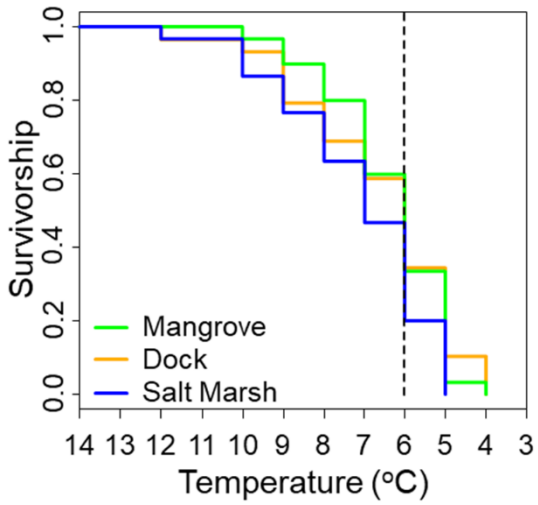

Figure 7.3. Kaplan-Meier curves comparing cold tolerances of *A. pisonii* from different habitats. Dashed line represents LD50.

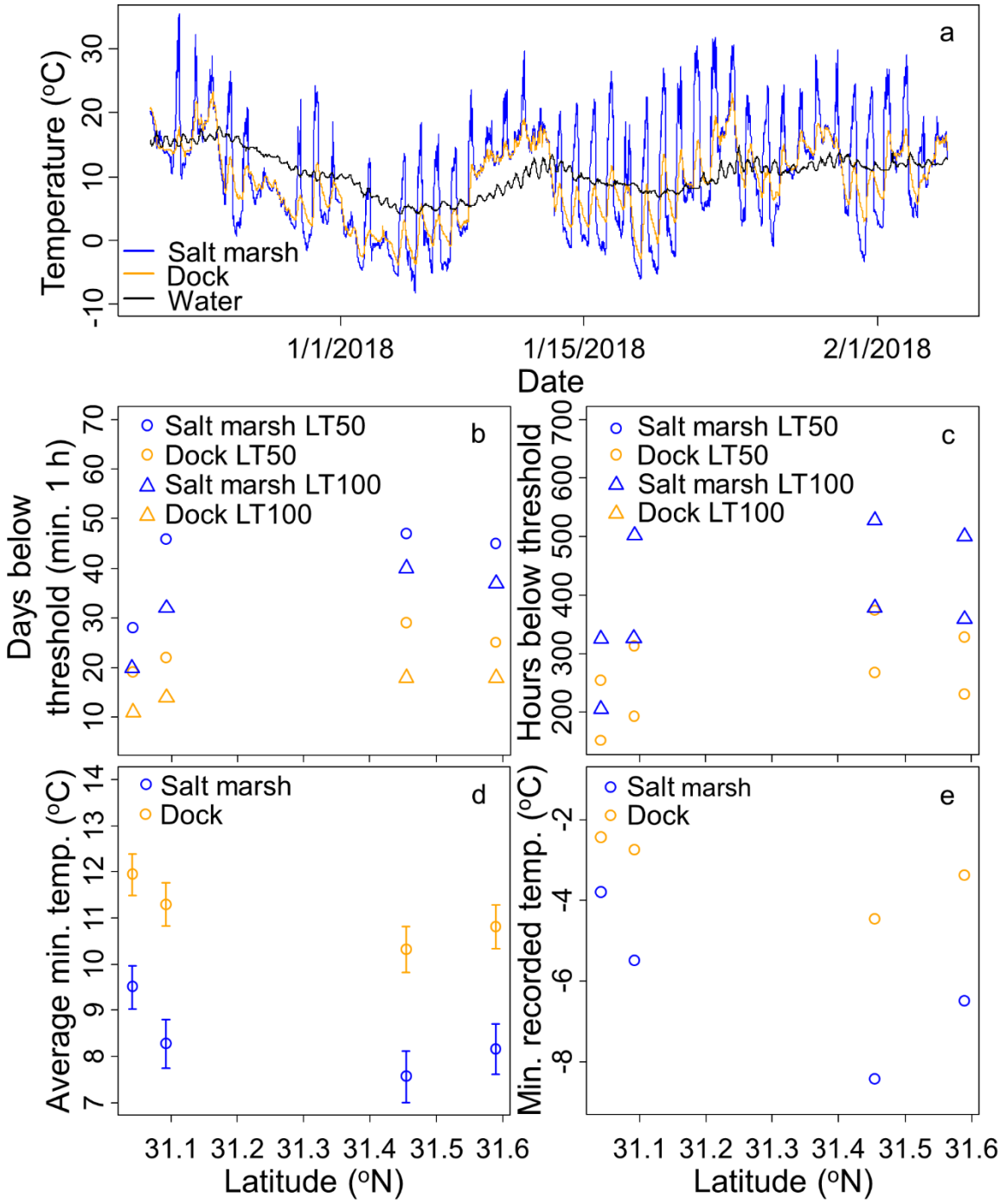

Figure 7.4. (A) Temperatures under a dock and in a nearby salt marsh at Sapelo Island. Water temperatures from a nearby climate station. (B) Days where the temperature remained below *A. pisonii* LT50 and LT100 for at least one continuous hour across habitats and sites. (C) Total hours below *A. pisonii* LT50 and LT100 for at least one continuous hour across habitats and sites. (D) Minimum daily temperatures (Mean±SE) recorded over the deployment period across habitats and sites. (E) Absolute minimum temperature recorded in each site/habitat

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CHAPTER 8

GENERAL CONCLUSION

8.1 Conclusion

In this dissertation we examined the variable effects of habitat, both natural and artificial, on the ecology, life history, and range expansion of a range shifting species within its historic and colonized ecosystems by addressing six key topics:

CHAPTER 2 described the loss of *A. pisonii* site fidelity and foraging foray behaviors in the colonized salt marsh ecosystem. This crab was shown to exhibit site fidelity to individual "home trees" in its historic mangrove habitat and to undertake regular foraging forays away from those trees in a pattern expected from a philopatric species. However, crabs in the salt marsh showed no evidence of exhibiting either behavior. As site fidelity is often associated with important ecological and life history events (Bollinger & Gavin 1989, Pomeroy et al. 1994, Cannicci et al. 1996, Driggers et al. 2014), the loss of this behavior is likely to negatively impact the ecology of *A. pisonii*. Further, fecal chemical cues appear to provide the mechanism for establishing site fidelity in the mangrove suggesting that this behavior is lost in the salt marsh due to tidal submersion of substrate preventing the establishment of these cues. Ultimately, this chapter demonstrates that structural differences between habitats can drive the loss of ecologically important behaviors in colonizing species.

CHAPTER 3 established the role of artificial docks within the salt marsh as an analogous habitat (*sensu* Lundholm & Richardson 2010) to mangroves by demonstrating that docks provide *A. pisonii* with improved conditions over the surrounding salt marsh in many, but not all, measured aspects. Compared to the mangrove, and in concordance with previous work (Riley & Griffen 2017), the salt marsh was shown to be a suboptimal habitat for *A. pisonii* in every measured aspect of the study. Most notably, crabs in the salt marsh were found to be smaller than conspecifics in either the dock or mangrove habitats. Given the importance of size for reproductive output (Leme & Negreiros 1998, López-Sánchez & Quintero-Torres 2015, Riley & Griffen 2017) and hierarchical positioning (Warner 1970), this decrease in size in the salt marsh could have cascading effects. Crabs in the salt marsh also experienced more irregular access to food and a lower quality diet than conspecifics in the mangrove and on docks; in fact, crabs on docks appear to have access to a higher quality diet than even those in the mangrove. Similarly, crabs in the saltmarsh experience a suboptimal thermal environment and exhibit riskier thermoregulatory behavior compared to conspecifics in the mangrove and dock habitats, both of which provide a cool shaded environment. Given the importance of diet and thermal conditions to an organism's ecology and life history (Leffler 1972, Huey 1991, Millamena & Quinitio 2000, Buck et al 2003, Griffen et al. 2008, Charron et al. 2015), this chapter both strengthens previous conclusions that the salt marsh provides a suboptimal habitat for *A. pisonii* and provides evidence that docks mitigate some of these negative impacts. Ultimately, this chapter demonstrated multiple mechanisms through which habitat effects can negatively impact a species in a novel ecosystem while also establishing the potential of artificial structures to mitigate many of these impacts.

CHAPTER 4 expanded on the findings of CHAPTER 3 by demonstrating the impact of habitat effects on the reproduction of *A. pisonii*. This chapter demonstrated that an artificial habitat within a suboptimal colonized ecosystem can increase the reproductive potential and fitness of a range shifting species. Crabs found on docks produced more eggs overall, more eggs per unit investment, and higher quality larvae than conspecifics in the surrounding salt marsh. Further, these differences appear to derive from disparities in diet-driven maternal reproductive investments. This was particularly clear through the examination of egg lipids as eggs originating from docks displayed higher concentrations of developmentally important fatty acids (Yamaoka & Scheer 1970, Cahu et al. 1995, Beltz et al. 2007, Rosa et al. 2007, Rey et al. 2017) than those from the salt marsh. Further, analyses of fatty acid trophic markers support the conclusions of CHAPTER 3 by suggesting that the high-quality reproductive investment made by crabs on docks derives largely from a diet high in animal material. Yet, despite the increased reproductive fitness of crabs on docks, those from the mangrove produced larvae of even higher quality. As eggs originating from the mangrove had the highest gross lipid content, this appears to be a result of a shift in reproductive strategy to quantity over quality in range-edge compared to the range-core populations; a strategy often exhibited by edge populations (Chuang & Peterson 2016). Yet, docks appear to allow *A. pisonii* to bridge these strategies by producing large numbers of intermediate quality offspring and thus may represent a theoretical "mid-range" reproductive habitat despite occurring at the range-edge. By mechanistically demonstrating the ability of docks to increase the reproductive potential and fitness of *A. pisonii* in the salt marsh, this chapter provides evidence that artificial analogous habitats could provide a vital reproductive boost for shifting populations.

CHAPTER 5 explored the how habitat structure can alter the magnitude of disturbance impacts. Through pre and post-storm field surveys, this chapter showed that large *A. pisonii* in the salt marsh ecosystem, both in the marsh proper and on docks, were disproportionately impacted by Hurricane Matthew. However, the size reduction in the dock habitat was driven by one site, suggesting docks provided some refuge from the storm. In contrast to the range-edge habitats, neither the mean size nor size frequency distribution of crabs found in the historic mangrove ecosystem changed as a result of the storm. This difference in size-specific mortality between the historic and colonized ecosystems may be a result of the negation of the climbing behavior that *A. pisonii* uses to avoid rising waters by the complete submergence of dock and salt marsh structure. Additionally, the lower structural complexity of these habitats compared to the mangrove may have further reduced the ability of large crabs to seek shelter from hurricane-force storm surge and currents. Given the relationship between size and reproduction in *A. pisonii* (López-Sánchez & Quintero-Torres 2015, Riley & Griffen 2017), the disproportionate impact of the storm on large crabs has the potential to negatively impact reproduction at the range-edge. Thus, this chapter suggests that habitat structure can directly mediate the disturbance impacts experienced by a range shifting species.

CHAPTER 6 demonstrated how habitat effects can alter ecologically important behaviors of range shifting species. Compared to the historic mangrove structure, the ecologically and socially important ritualistic aggression behavior of *A. pisonii* was altered on salt marsh and dock structures. Interactions were more likely to occur on salt marsh structure than mangrove or dock structures and those interactions were more dangerous on salt marsh and dock structures than mangroves. Despite the similar danger

of interactions on dock and salt marsh structure, dock structure lowered the incidence of interactions and allowed for greater possibility of retreat, suggesting docks provide an improved substrate over marsh grasses for performing this behavior. Further, crab morphology greatly impacted the outcome and occurrence of ritualized aggressions. As in many species (Caldwell & Dingle 1979, Gabbanini et al. 1995, Sneddon et al. 1997), larger individuals and those with relatively larger claws were more likely to win an interaction. This was of direct relevance to inter-habitat interactions due to the difference in claw morphology between habitats. While the relatively large claws of crabs from docks was expected as a result on their high-carnivory diet (Smith & Palmer 1994), the still larger relative claw size of crabs from the salt marsh was unexpected given the low-quality, low-carnivory diet of this population. Whether the relatively large claws of salt marsh crabs are a result of a response to alterations to the behavior itself, the structure of marsh grasses, or a bioenergetics factor is uncertain. Ultimately, the alteration of ritualistic aggression due to differences in habitat structure and habitat-driven changes in claw size highlight how habitat effects experienced by range shifting species within novel ecosystems can interact in unexpected ways.

CHAPTER 7 provided conclusive evidence that the artificial dock habitat acts as a stepping stone refuge for *A. pisonii* by passively increasing the rate and extent of its range expansion over what would otherwise be possible in the salt marsh. After the winters of 2016-‘17 and ’17-‘18 crabs were found on docks 36 km and 22 km further north than elsewhere in the salt marsh. Further, the mechanism behind the ability of docks to aid this range expansion is the thermal refuge that they provide, not a difference in cold tolerance between mangrove, salt marsh, and dock populations. In fact, despite the abnormally cold

conditions during the winter of 2017-'18, temperatures under docks were consistently 2-5^{o}C warmer than the surrounding salt marsh. This chapter also adjusted the rate of *A. pisonii* range expansion from 62 km/decade (Riley et al. 2014) to 58 km/decade highlighting the importance of encompassing extreme events when attempting to predict the rate and extent of range shifts. Ultimately, this chapter demonstrated the critical role that artificial habitats can play in the range expansions of native species into novel ecosystems.

Collectively, this dissertation provides important insights into habitat effects on the ecology of range shifting species. It explored habitat effects on a range of important aspects of a shifting species' ecology and life history to show that artificial habitats have the potential to increase the ability of shifting native populations to survive and expand into an otherwise suboptimal novel ecosystem. This dissertation documented the alteration of ecologically important behaviors by novel habitat structures (CHAPTERS 2, 3 and 6) and the potential for artificial habitat analogues to mitigate some of these changes (CHAPTERS 3 AND 6). It further explored the potential of artificial habitats to mitigate a number of ecological and life-history impacts incurred by a native species as a result of interactions with a novel ecosystem (CHAPTERS 3 and 4). It also mechanistically showed how an artificial habitat analogue can increase the reproductive potential and fitness of a shifting species experiencing a suboptimal reproductive environment within a colonized ecosystem (CHAPTER 4). Additionally, it documented how habitat type and structure can alter the impacts that range shifting species experience as a result of a natural disturbance (CHAPTER 5). Finally, it demonstrated that an artificial habitat analogue acts as a stepping stone refuge to passively increase the rate and extent of a native species' range expansion

into a novel ecosystem (CHAPTER 7). This dissertation mechanistically explored a wide range of habitat effects on the ecology and life history of a native species expanding into a novel ecosystem and highlighted the role that artificial habitat analogues may play in mitigating negative impacts resulting from those effects. Thus, this dissertation emphasizes the need to mechanistically explore and consider habitat-level effects, including those of anthropogenic structures, when predicting, modelling, and managing current and future range shifts.

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APPENDIX A:

SUPPLEMENTAL TABLES AND FIGURES FOR CHAPTER 3[1]

A1.1 Tables

Table A.1. Name, habitat type, and location of site in latitude-longitude coordinates. The groups of crabs observed for behavior at each site is also included.

Site	Habitat	Lat-Long	Groups of Crabs Observed
Round Island Park	Mangrove	27°33'33"N 80°19'53"W	1
Pepper Park	Mangrove	27°29'42'N 80°18'12"W	3
Oslo Park	Mangrove	27°35'14"N 80°21'55"W	2
North Causeway Park	Mangrove	27°28'28"N 80°19'12"W	2
Bear Point	Mangrove	27°25'48"N 80°17'10"W	2
GTM NERR	Saltmarsh	30°0'49"N 81°20'42"W	12
Anastasia State Park	Saltmarsh	29°52'40"N 81°16'32"W	4
Palm Valley	Dock	30°7'57"N 81°23'8"W	5
Yacht Club	Dock	29°53'9"N 81°17'8"W	3

[1] Cannizzo ZJ, Dixon SR, & Griffen BD. 2018. An anthropogenic habitat within a suboptimal colonized ecosystem provides improved conditions for a range-shifting species. *Ecology and Evolution*. 8: 1524-1533.
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A1.2 Figures

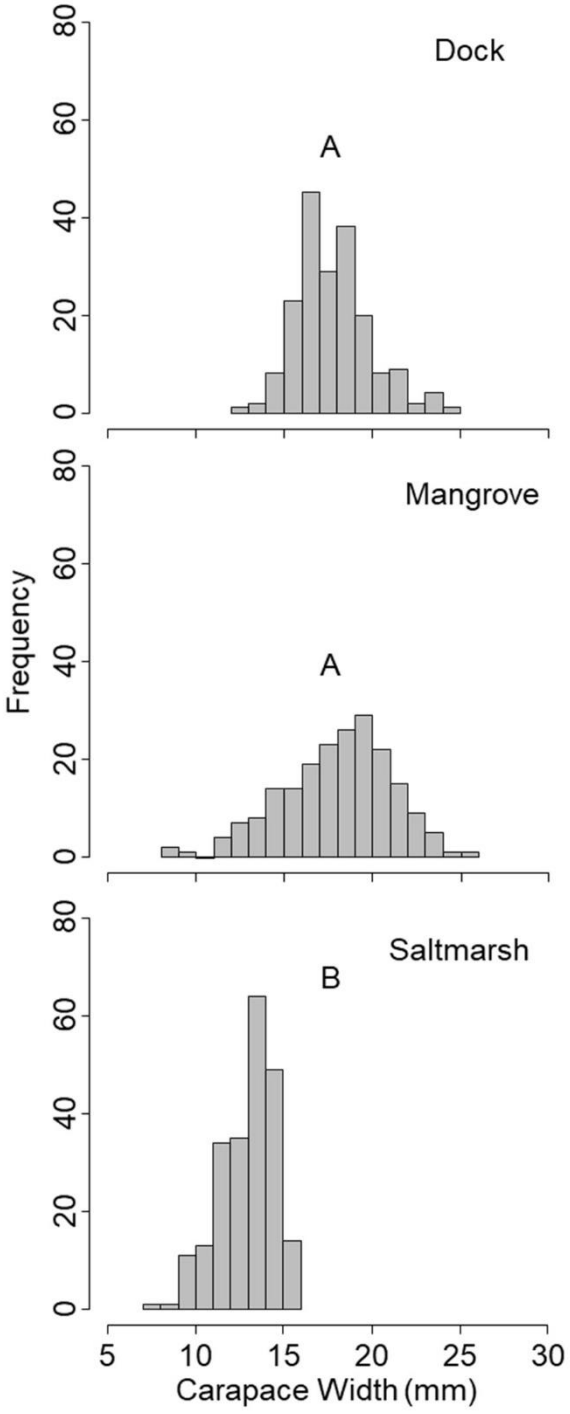

Figure A.1. Size frequency distributions of *A. pisonii* in each of the three habitat types. Groups that are significantly different are denoted by different letters.

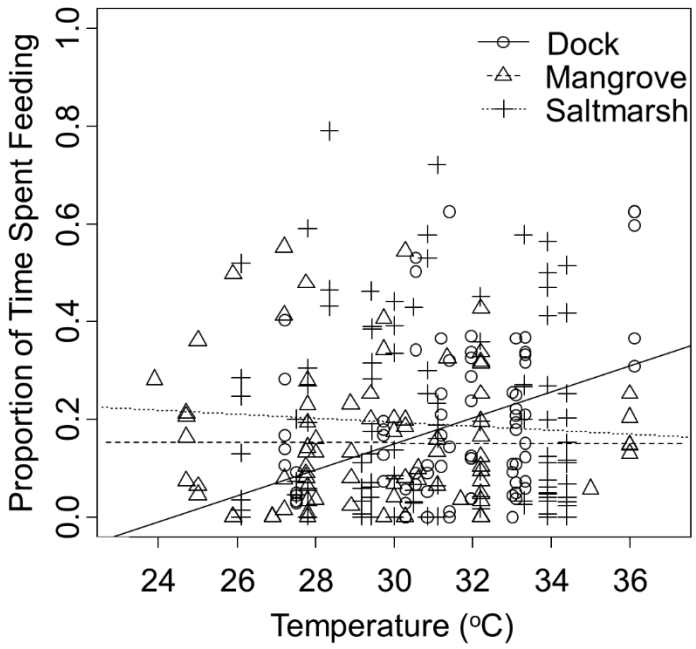

Figure A.2. Relationship of the proportion of time crabs in each habitat spent feeding and ambient temperature. Lines show slopes of relationships for each individual habitat.

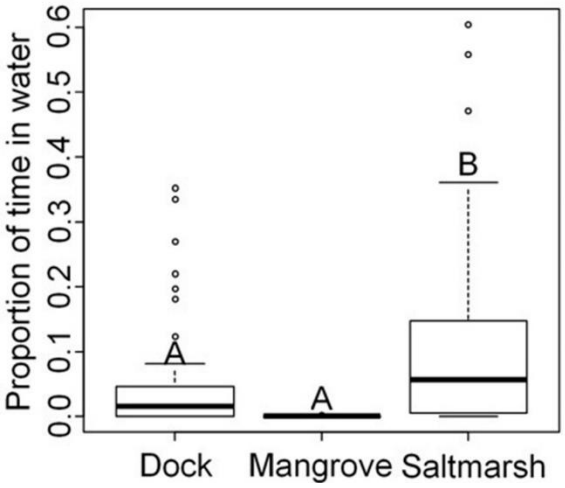

Figure A.3. Boxplots of the proportion of time spent in the water by crabs in each of the habitats. Groups that are significantly different are denoted by different letters.

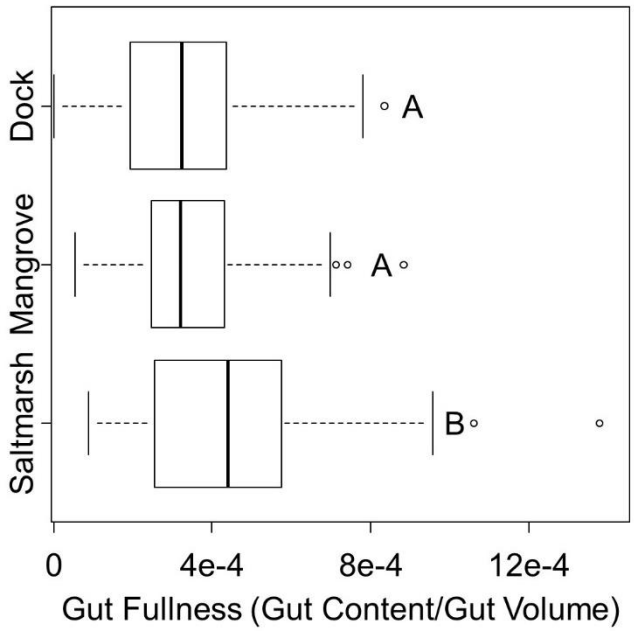

Figure A.4. Boxplots comparing the tide-independent gut fullness of *A. pisonii* between habitats. Groups that are significantly different are denoted by different letters.

APPENDIX B:

METHODOLOGICAL SUPPLEMENT FOR CHAPTER 4

B.1 Sample Storage

Unless otherwise stated, all materials used throughout these methods were acid-washed and all glass was combusted. After being removed from the pleopods of the mother (see Methods section of main paper), the whole egg clutch was placed in a glass vial with a Teflon cap. The sample was then freeze-dried and stored at -80^{o}C until analysis.

B.2 Lipid Extraction

Lipids were extracted from the eggs using a modified Folch extraction on a 0-40mg subset of eggs (Folch et al. 1957, Hara & Radin 1978, Undeland et al. 1998). The remaining egg clutch was returned to -80^{o}C storage. During extraction, a known quantity of C24 alkane was added as a recover standard. Finally, at the end of the extraction the combined lipid/solvent mixture was then placed under a steady stream of Nitrogen gas to evaporate the solvent. Once dried, the remaining lipid was weighed to obtain the gross lipid mass. The vial was then capped with nitrogen and stored at -80^{o}C until fatty acid methylation could be performed (< 2 weeks).

B.3 Fatty Acid Methylation

The fatty acids in the extracted lipids (see above) were methylated through a modification of the methods of Morrison and Smith (1964). The sample was first thawed

to room temperature while a 0.5 N KOH solution was prepared by dissolving 28mg of KOH in 1ml of methanol. 1ml of 0.5N KOH was added to the sample which was then vortexed for ~30s. The sample was then placed in a sand bath and heated for 15min at 70^{o}C. After being removed from heat, 1ml of 14% Boron Triflouride was added to the sample which was then returned to the sand bath for 5min. The sample was then allowed to cool to room temperature at which time 2ml of HPLC-grade hexane and 2ml of ultra-pure water, filtered with a Milli-Q Reference A+ system, was added. This mixture was vortexed for ~30s and allowed to stand until it separated into two layers. While the sample may be separated with a centrifuge, it was not necessary for this study. The top (lipid/solvent) layer was then transferred to a new vial and capped with a Teflon cap. The hexane-water wash was repeated twice more on the remaining water layer combining the lipid/solvent layers after each wash. The combined hexane-lipid layer was then capped with nitrogen and stored at -80^{o}C until volume correction (<48 Hours).

For volume correction, the sample was first thawed to room temperature at which time its volume was reduced to ~2ml by evaporating the solvent under a stream of Nitrogen gas. Next, the sample was transferred at a volumetric flask and HPLC-grade hexane was added until the sample was brought to 5ml. The sample was then transferred back to its vial and stored at -80^{o}C until interrogation via gas chromatography-mass spectrometry (GC-MS).

B.4 Sample Analysis via GC-MS

After being thawed, 2µl of the fatty acid methyl ester-hexane solution was interrogated via GC-MS on an Agilent Technologies 6890N Network equipped with a

30m Restek FAMEAX column with a 0.25mm internal diameter and a 0.25μm film thickness. This was connected to an Agilent 5975 Network Mass Selective Detector (electron ionization mode at 70eV and full scan mode 50-400 t 1.1 scans s^{-1}). The oven temperature was programed for an initial temperature of 70ºC followed by a linear increase to 200ºC at 10ºC min^{-1} and a second linear increase at 4ºC min^{-1} until 250ºC which was held for 10 min. The injector was set at 250ºC with the transfer line at 225ºC. Helium was used as the carrier gas at a flow rate of 1ml min^{-1}.

The fatty acids (FA) were then identified by comparing retention times to known FAs of a Supelco 37 Component FAME Mix. The peak area of each FA was obtained using Agilent ChemStation software. The concentration of each FA was then calculated from a dilution curve created from the Supelco 37 Component FAME Mix spiked with a known concentration of recovery standard. The FA peak areas were first normalized to recovery standard then concentrations were determined using the regression curves of the external standards.

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APPENDIX C:

SUPPLEMENTAL TABLES AND FIGURES FOR CHAPTER 4

C.1 Tables

Table C.1. Statistical output for results presented in the main text. Asterisks denote significant p-values (see main text of CHAPTER 4).

Demographics of Ovigerous Females		
Statistical Test:	*ANOVA*	
$F_{2,293}$	213.6*	
Reproductive Energy Investment		
Statistical Test:	*ANOVA*	
Sex/Reproductive Stage	**(df) F-value**	
Males	(2,143) 17.01*	
Ovigerous Females	(2,110) 17.01*	
Non-Ovigerous Females	(2,131) 12.11*	
Larval Starvation Resistance		
Statistical Test:	*Cox Proportional Hazards*	
Explanatory Variable	**z-value**	
Maternal Size	-3.21	
GW:CW	-0.34	
Mangrove vs Dock	3.25*	
Mangrove vs Salt Marsh	5.80*	
Dock vs Salt Marsh	2.63*	
Larval Size at Hatching		
Statistical Test:	*Linear Mixed Model*	
Explanatory Variables	**Estimate**	**z-value**
Maternal Size	0.0119	1.241
GW:CW	25.711	2.335*
Dock vs Salt Marsh	0.201	0.280
Dock vs Mangrove	-0.219	-0.523
Mangrove vs Salt Marsh	0.0119	0.641
Clutch Size		
Statistical Test	*ANOVA*	
$F_{2,146}$	30.34*	
Size-Independent Clutch Size		
Statistical Test:	*Linear Model*	
Explanatory Variable	**Estimate**	**z-value**
GW:CW	-20689	-1.095

Mangrove vs Dock	1247.9	2.095*
Mangrove vs Salt Marsh	1239.5	2.140*
Dock vs Salt Marsh	-8.404	-0.015
Egg Energy Content		
Statistical Test:		*Linear Model*
Explanatory Variable	**Estimate**	**z-value**
Maternal Size	0.026	0.415
GW:CW	3.645	0.349
Non-eyed vs Eyed Eggs	1.619	5.526*
Dock vs Mangrove	0.013	-0.037
Dock vs Salt Marsh	-0.321	-0.743
Mangrove vs. Salt Marsh	-0.304	-0.633
Gross Lipid Content		
Statistical Test:		*Linear Model*
Explanatory Variable	**Estimate**	**z-value**
Maternal Size	-0.113	-0.755
GW:CW	-1.712	8.151
October vs June	4.391	4.928*
October vs August	3.379	3.702*
Mangrove vs Salt Marsh	-2.565	-3.774*
Mangrove vs Dock	-3.442	-5.064*
Dock vs Salt Marsh	3.450	0.352
Omega-3 Fatty Acid Concentration of Eggs		
Statistical Test:		*Linear Model*
Explanatory Variable	**Estimate**	**z-value**
Dock vs Mangrove	-0.005	-4.044*
Dock vs Salt Marsh	-0.003	-3.628*
Mangrove vs Salt Marsh	0.002	1.321
EPA Concentration of Eggs		
Statistical Test:		*Linear Model*
Explanatory Variable	**Estimate**	**z-value**
Dock vs Mangrove	-7.062e-3	-8.997*
Dock vs Salt Marsh	-3.004e-3	-2.913*
Mangrove vs Salt Marsh	4.085e-3	3.458*
October vs June	-2.873e-3	1.994*
DHA Concentration of Eggs		
Statistical Test:		*Linear Model*
Explanatory Variable	**Estimate**	**z-value**
Dock vs Mangrove	-1.802e-3	-8.769*
Dock vs Salt Marsh	-1.574e-3	-5.831*
Mangrove vs Salt Marsh	2.277e-4	0.741
ALA Concentration of Eggs		
Statistical Test:		*Linear Model*
Explanatory Variable	**Estimate**	**z-value**
Mangrove vs Dock	-3.999e-3	-5.136*
Mangrove vs Salt Marsh	-2.643e-3	-2.271*
Dock vs Salt Marsh	1.355e-3	1.325

HUFA Concentration of Eggs		
Statistical Test:	*Linear Model*	
Explanatory Variable	**Estimate**	**z-value**
Dock vs Mangrove	-9.793e-3	-8.778*
Dock vs Salt Marsh	-4.677e-3	-3.191*
Mangrove vs Salt Marsh	5.12e-3	3.097*
October vs June	-2.873e-3	1.994*
October vs July	-3.719e-3	-2.661*
Omega-3:Omega-6 Ratio of Eggs		
Statistical Test:	*Linear Model*	
Explanatory Variable	**Estimate**	**z-value**
Maternal Size	0.067	2.088*
Mangrove vs Dock	0.303	1.803
Mangrove vs Salt Marsh	-0.146	-0.580
Dock vs Salt Marsh	-0.449	-2.032*
EPA:DHA Ratio of Eggs		
Statistical Test:	*Linear Model*	
Explanatory Variable	**Estimate**	**z-value**
Salt Marsh vs Dock	-6.296	-5.900*
Salt Marsh vs Mangrove	-4.847	-3.991*
Dock vs Mangrove	1.450	1.785
OFA Concentration of Eggs		
Statistical Test:	*Linear Model*	
Explanatory Variable	**Estimate**	**z-value**
GW:CW	-0.021	-2.340*
Salt Marsh vs Dock	-1.210e-3	-2.391*
Mangrove vs Dock	8.230e-4	1.429
Mangrove vs Salt Marsh	-3.874e-4	1.006
Egg Glycogen Content		
Statistical Test:	*Linear Model*	
Explanatory Variable	**Estimate**	**z-value**
Maternal Size	-1.551e-5	-3.703*
GW:CW	-1.252e-4	-0.508
Dock vs Mangrove	3.478e-5	1.620
Dock vs Salt Marsh	2.405e-5	0.841
Mangrove vs Salt Marsh	-1.074e-5	-0.328

Table C.2. Full results of fatty acid analyses. Fatty acid name and C:Dn-x code (# Carbon atoms:# double bonds n-location of first double bond; c/t signifies cis/trans). Average weight percent of each compound per egg±SD in each habitat, with letters and colors representing homogeneous groups between habitats within each row. P-value of maternal size and GW:CW, +/- represent direction of effect. Effect of month (LM: $p<0.05$) represented by month number and direction of effect.

Fatty Acid	C:Dn-x	Mangrove	Dock	Saltmarsh	Size	GW:CW	Month
Myristic	14:0	0.204±0.060^{A}	0.230±0.0001^{A}	0.194±0.063^{A}	0.628	0.792	8>6; 8>7; 10>6; 10>7; 10>9
Myristoleic	14:1	0.017±0.021^{A}	0.014±0.016^{A}	0.009±0.012^{A}	0.319	0.948	---
Pentadecanoic	15:0	0.100±0.033^{A}	0.081±0.036^{B}	0.119±0.059^{A}	0.816	0.011 (-)	10>6; 10>9
cis-10-Pentadecanoic	15:1	0.032±0.017^{A}	0.022±0.015^{A}	0.033±0.035^{A}	0.469	0.155	10>9
Palmitic	16:0	3.350±0.833^{A}	3.047±0.750^{A}	3.103±0.931^{A}	0.869	0.628	10>6; 10>7
Palmitoleic	16:1	1.993±0.713^{A}	1.830±0.604^{A}	1.612±0.548^{A}	0.248	0.389	10>7
Heptadecanoic	17:0	0.105±0.047^{A}	0.126±0.036^{A}	0.148±0.080^{A}	0.412	0.084	9>6
cis-10-Heptadecanoic	17:1	0.140±0.048^{A}	0.127±0.044^{A}	0.133±0.077^{A}	0.112	0.145	---
Stearic	18:0	0.466±0.141^{A}	0.468±0.140^{A}	0.535±0.429^{A}	0.222	0.839	10>6; 10>7; 10>8
Oleic/Elaidic	18:1n9c/t	0.868±0.228^{A}	0.438±0.119^{B}	0.417±0.141^{B}	0.617	0.328	10>6
Linoleic	18:2n6c	0.641±0.253^{A}	0.643±0.237^{A}	1.042±0.564^{A}	0.102	0.706	9>6; 9>8
Linolelaidic	18:2nt	0.011±0.016^{A}	0.030±0.049^{A}	0.035±0.076^{A}	0.877	0.320	---
gamma-Linoleic	18:3n6	0.012±0.046^{A}	0.041±0.061^{A}	0.047±0.078^{A}	0.944	0.366	---
alpha-Linoleic	18:3n3	0.793±0.401^{A}	0.397±0.149^{B}	0.474±0.215^{B}	0.621	0.397	---
Arachidic	20:0	0.023±0.050^{A}	0.020±0.046^{A}	0.029±0.068^{A}	0.941	0.250	---
cis-11-Eicosenoic	20:1n9	0.021±0.009^{A}	0.025±0.017^{A}	0.018±0.018^{A}	0.403	0.389	10>6; 10>7; 10>8; 10>9
cis-11,14-Eicosadenoic	20:2n6	0.020±0.010^{A}	0.031±0.018^{B}	0.030±0.011^{B}	0.676	0.906	9>6
cis-8,11,14-Eicosatrienoic	20:3n6	0.021±0.047^{A}	0.019±0.012^{A}	0.034±0.051^{A}	0.951	0.090	---

cis-11,14,17-Eicosatrienoic	20:3n3	0.032±0.023^{A}	0.025±0.008^{A}	0.022±0.010^{A}	0.110	0.602	9>6
Arachidonic	20:4n6	0.099±0.041^{A}	0.201±0.086^{B}	0.217±0.126^{B}	0.176	0.177	9>6
cis-5,8,11,14,17-Eicosapentaenoic	20:5n3	0.258±0.128^{A}	0.981±0.384^{B}	0.703±0.301^{C}	0.642	0.747	10>7
cis-4,7,10,13,16,19-Docosahexaenoic	22:6n3	0.055±0.031^{A}	0.230±0.118^{B}	0.066±0.036^{A}	0.612	0.692	---

C.2 Figures

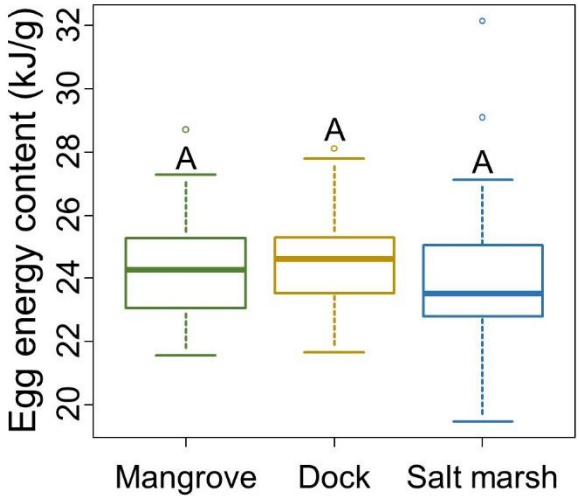

Figure C.1. Gross energy content of eggs originating from each habitat.

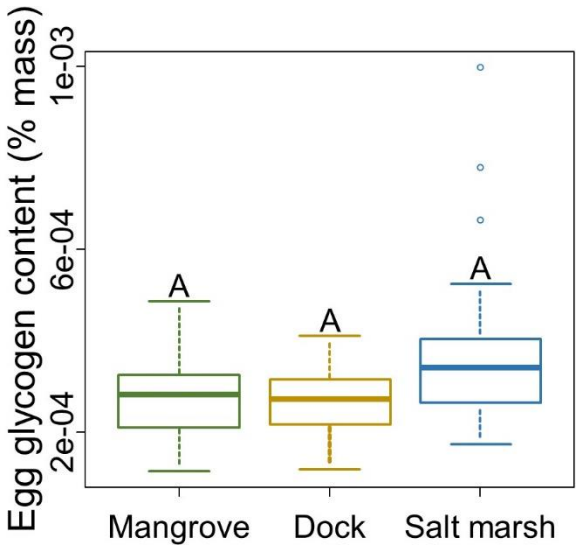

Figure C.2. Glycogen content of eggs originating from each habitat.

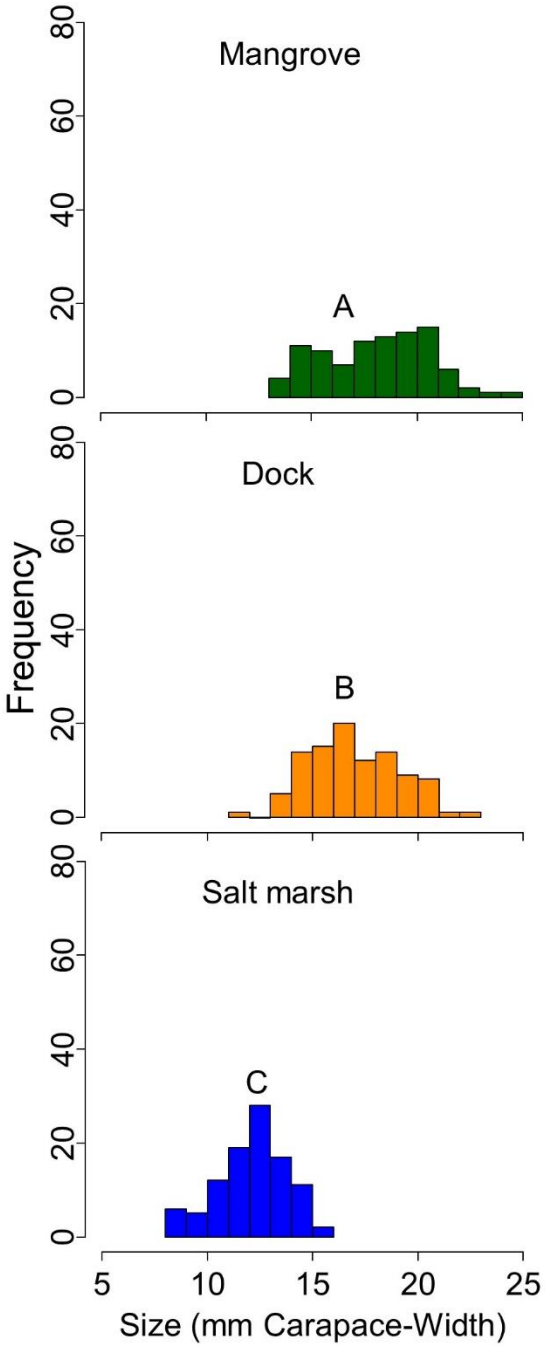

Figure C.3. Size frequency distributions of ovigerous females in each habitat. Letters represent homogeneous groups in relation to average size and size frequency distributions.

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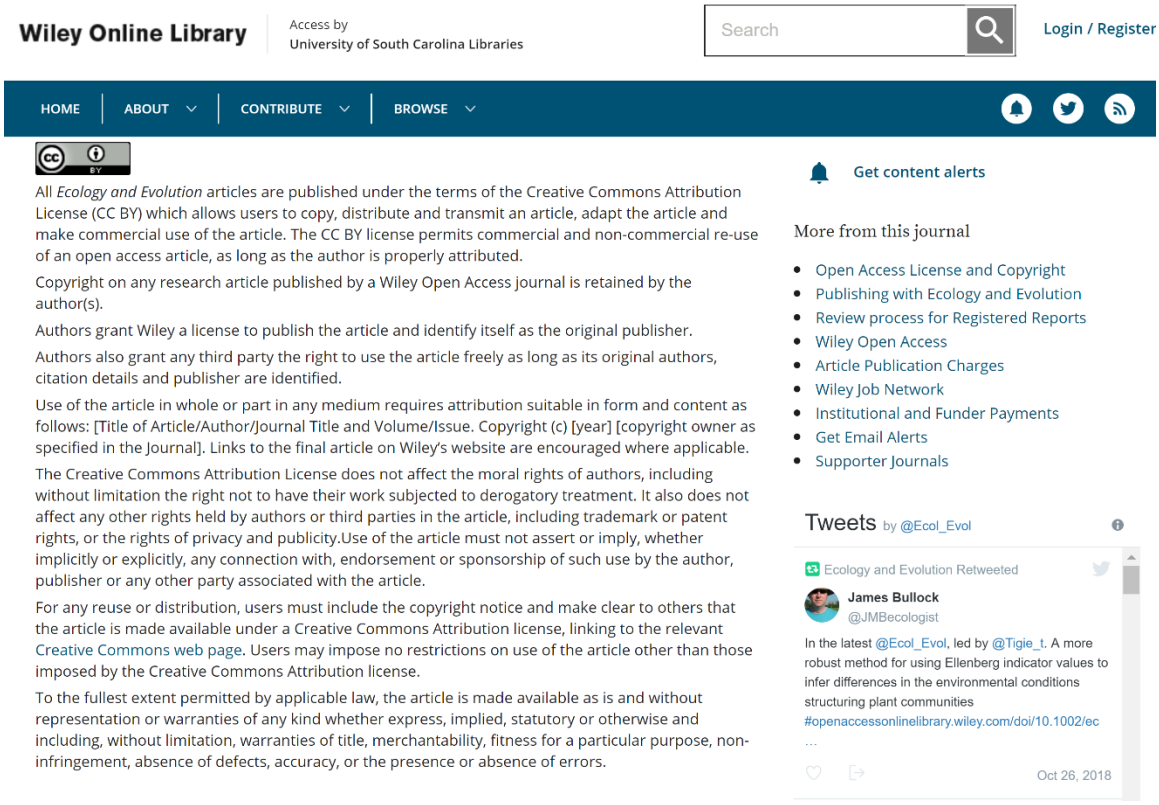

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